THE DISPERSAL OF PLANTS

THROUGHOUT

THE WORLD

BY

HENRY N. RIDLEY, M.A., C.M.G., F.R.S., F.L.S.
Corresp. Member of Zoological and Pharmaceutical
Societies, etc. Late Director of Botanic Gardens,
Straits Settlements.

Illustrations by
MISS M. B. MOSS and the AUTHOR

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INTRODUCTION

THE study of the Dispersal of Plants—whether by seeds or by vegetative portions—is one of very great importance in its bearing on the distribution of plants throughout the world, the causes of their presence or absence in different localities, the changes of floras at different periods, and all that goes to make a local flora. It has also been an important factor in the evolution of species, genera, and, in some cases, even of orders. In these respects it is of more importance than the modifications of species for insect—or wind—fertilisation, a subject on which there are several fairly complete treatises. For while few plants suffer to any extent, from want of pollination, by the absence of an essential pollinator, the migration of plants—in their struggle for existence—is often checked or accelerated by modifications for dispersal, or the want of them.

It is therefore remarkable that there is no adequate work on the subject of Dispersal. It is true that a large number of observations and records have been made, from time to time, for many years by various naturalists; but these are scattered over a great number of books, journals, and other publications, and have never been brought together into one work, so as to be easy to study, and to obtain deductions from them as to the meaning and import of the modifications of fruit and seed.

This book is an attempt to collate and compare the observations and records on the subject. I have sought information in all publications procurable in which there are, or might be, observations bearing on the subject. There are probably many more lying latent in obscure and often inaccessible literature, which I have been unable to discover. I have had the opportunities of research in the libraries of Kew Gardens, the Natural History Museum, and the Linnean Society, for information on this subject.

To this I have added a considerable amount of evidence derived from my own observations in many parts of the world, over a long period of years, and I have been assisted not a little by many naturalists and observers, both in temperate and tropical regions, who have supplied me with notes and records relating to the subject.

The complete story of dispersal, however, is not yet finished, and there is still a large field of work for observers. Indeed, I have some hopes that this work may stimulate others to watch for, and record, facts bearing on the migration of plants in all parts of the world. Travellers in almost any area of the globe, but especially in the tropics, may easily add to our knowledge of this subject. I have often received valuable information from people who would not lay any claim to be called scientific. In fact, this class of Nature study merely demands a power of accurate observation on the part of anyone who happens to have the facilities for travel in any country. It is, of course, in the less well-known large areas, such as Africa, tropical and temperate Asia, South America and Australia, that the most valuable researches are still to be made, but there remains much to be done in the better-known and more thickly-populated regions.

It must be realised that every plant we find in any spot, or one of its ancestors, must somehow have contrived to get into the locality in which we observe it to be, and the question to be answered is: How did it arrive and establish itself there?

Nomenclature.

Throughout this work I have used the old-fashioned scientific names of plants and animals as popularly employed before the system of modern alterations in nomenclature came into use, as it is easier to understand what plant or animal is referred to by these names. In the case of genera (which are very plastic at the present epoch, and of which often a vast number of species have been described and named, such as *Hieracium*, *Taraxacum*, or *Rubus* (the R. *fruticosus* section), I have used the general name in a large sense to cover all the minutely differing forms classed by some as species, e.g., *Taraxacum dens-leonis* for all the Dandelions.

The valuation of the term " species " varies largely with different botanists, and in a study of the natural history of plants as this is, it is more convenient to classify the minutely varying forms of these plastic plants as all of one species.

A large number of really unnecessary new words have been invented in oecological works for all kinds of conditions, states, and phenomena of dispersal and distribution. These I have excluded altogether, except where they actually convey a fact or theory which cannot be stated otherwise than by a long sentence; of such as I use, the actual meaning is explained in its proper place, and here I may state that I use the words " Dispersal " and " Dissemination " as meaning the methods by which the plant is diffused or transported from place to place, and " Distribution " to signify the results of the dispersal agents, namely, the actual localisation of the plants in the world in the present epoch or, so far as we know it, in past epochs.

History of the Migrations of Plants.

The wanderings of plants about the world have existed ever since their first evolution, and are still continuing.

In the very earliest days the minute cellular organisms moved about in water by rain-wash, streams, or sea currents, and on land by wind blowing them far and wide over the world, as many plants are disseminated at the present day. In the development of the *Vascular cryptogams*, *Ferns*, *Mosses*, *Equisetaceae*, *Lycopodiaceae*, etc., the wind played far the greater part in covering the world with vegetation.

In the Secondary Period the evolution of the great herbivorous terrestrial Reptiles doubtless added another factor to the means of seed-dispersal, by their swallowing the fruits and passing the seed, or by the adherence of seed to their feet in mud; but practically nothing seems known of the habits of these creatures, although we know that the great tortoises of the Galapagos Islands, and some of the lizards, do disperse the seeds of plants in this way at the present day (*see* Chapter V, on Reptiles).

The Tertiary Period, with its great evolution of fruit-eating Birds and Mammals, was accompanied by a very extensive evolution of plants with drupaceous and baccate fruits.

The superb red and yellow colouring of so many of our fruits was brought about by the competition of the fruit-eating birds for food, much as the colouring of the flowers was due to the exactions of honey-seeking insects—

bees and butterflies. To the then abundant herbivorous mammals we probably owe the evolution of the grasses, and their distribution and abundance, as well as many of the smaller herbaceous plants, in eating which they swallowed and passed the seeds. Besides these, we owe the evolution of the plants, mostly small with adhesive fruits, which they transported from place to place in their wanderings, attached to their feet or bodies.

In the Quaternary Period we have the gradually-increasing action of MAN, wandering from island to island, and from continent to continent, carrying with him, intentionally or accidentally, seeds and plants from place to place, and altering in many localities the whole flora of the area which he occupied. In many cases he almost entirely destroyed the original flora of a country as he found it, and substituted for it plants which he brought from other parts of the world in his wanderings.

Exterminating the great herds of wild animals by hunting, and destroying their feeding-grounds by agriculture, he replaced them to some extent by flocks and herds, which disseminated many plants over the areas in which he fed and drove them, much as the wild animals had done before he came.

Many species have undoubtedly been exterminated by the felling and burning of the forests, by draining lakes and marshes, and by agriculture, and have been replaced by cultivated plants and their concomitant weeds. Many plants which, before the advent of man, were certainly local and of limited area, are now very abundant as weeds in all parts of the world, being adapted to the changed environment due to the advent of man. The story of some of these will be found under the account of Dispersal by Human Agency (Chapter IX).

These changes of flora due to human agency began in many places where man had passed out of what may be called the "hunter" era, very many thousand years ago—in Europe in Neolithic days, in India, Ceylon, Egypt, Asia Minor, China, and Polynesia, in prehistoric days, probably 4000 or 5000 years B.C., or before that.

But this alteration of the original floras was vastly increased when the world began to be more thoroughly explored and colonised in the 16th and 17th centuries, and only attained its maximum within the last two hundred years. There are still many areas (of comparatively small size, for the most part) where man has as yet made no change, such places as the interior of the Malay Peninsula and of tropical South America, but the destruction of the original floras and substitution of cultivated plants and weeds from all parts of the world is still continuing. In many places in the Malay Peninsula where, in 1889, there were dense, almost impenetrable forests of Malayan trees, shrubs and herbs, now—35 years later—not one original plant is to be seen, the country being covered with the American *Hevea* and other introduced plants.

Changes due to Alterations in Climate and Environment.

Floras have also been changed by alterations of climate and, more frequently, by alteration of environment, soils, humidity, excess or reduction of light, and other factors, and also by the changes in the relative positions of land and sea.

Nature never allows an area on which plants can grow to remain bare for any appreciable length of time. The competition of plants for fresh and suitable places of growth is too great to allow of any delay. There is a constant invasion of seeds and spores in vast quantities to all parts of the globe, and those that reach the vacant spaces first, and have the greatest power of adaptability to circumstances, are the first occupiers of the new ground. Of the seeds

produced by plants, the greater part in almost every case perish, generally from want of adaptability to climate and environment, and many also from want of adequate means of dispersal.

An island rises out of the sea : within a year some plants appear on it, first those that have sea-borne seeds or rhizomes, then wind-borne seeds, then those borne on the feet and plumage of wandering sea-fowl, and when the vegetation is tall enough, come land birds bringing seeds of the baccate or drupaceous fruits which they had eaten before their flight. Finally appears man with seeds of his food crops and the weeds which accidentally accompany them, or are carried by his domestic animals.

If, owing to the denudation of mountains by rain and river, the land of a continent increases in size by the deposition of the washed-down silt into the sea, no sooner is the deposit raised above the surface of the water than there appear maritime plants, sea-borne from the neighbouring coasts. As the soil becomes firmer and higher, and the salinity diminishes, seeds washed down from the interior, wind-borne seeds of *Compositae*, spores of ferns, and the minute seeds of orchids, germinate and establish themselves, while the first-comers are often forced out by the changes of environment. Birds and mammals bring other plants, and the ground is sooner or later covered with a large and varied flora.

Occasionally one finds on Downs spots where turf has been dug away and the soil left bare. Within a surprisingly short time they are dotted over with a vegetation derived mainly from seeds blown along the downs. Thus one finds these spots covered with such plants as *Crepis*, *Hieracium*, *Sonchus*, with plumed fruit, *Plantago lanceolata*, *Thymus*, etc., to which, if the slope is suitable, are added such small plants as those whose seeds can be brought by rain-wash —*Asperula cynanchica*, *Erythraea*, *Lotus*, etc. These, however, usually come later than the wind-blown seeds. One has, however, to take into account the possibility of seeds lying dormant in the soil, as they often do, and germinating only when exposed to sun and rain, free from competition with other plants. Still, it is remarkable that the first and most abundant plant is *Plantago lanceolata*, commonly dispersed by wind, its long flexible peduncle giving it an advantage over the lower-growing herbs of the turf.

During the ages since plants were first evolved, many changes in climate have taken place in most parts of the world. Large areas in the north and south have been covered with ice (the Glacial Periods), causing the disappearance of nearly all the plants formerly occupying the ground. After the disappearance of the ice, the cleared ground was speedily covered again by plants whose seeds were disseminated by Wind, Water or Animals. In other parts of the world the forests disappeared from a failure of the rainfall, and became deserts, only carrying such plants as could become modified so as to grow under desert conditions, the seeds of which were disseminated from neighbouring countries. Not rarely a xerophytic country has been so altered by increased rainfall as to become a tropical rain-forest area. The rise of mountains or of islands, destruction of the flora by volcanic eruption, and many other large changes, have altered the flora or allowed the evolution of a new one. Besides these, the soil, water-supply, formation of the ground, and raids of insects and fungi are incessantly acting in small areas to alter the environment. These changes are continuous in most countries, and frequently, if only locally, affect the flora. As these changes go on, some plants disappear and others take their place as their seeds—dispersed over the ground—find a suitable habitat. As a rule, if no change takes place, the area is soon filled with vegetation, so that no intruders can push in, then there becomes a state of equilibrium, and the actual constituents of the flora may remain, covering the ground for a very long period.

Competition.

The number of seeds produced by certain plants is enormous, and that of some species is given on pp. 43 and 52. Of these seeds, far the greater number perish, through not reaching a suitable spot for germination and development. The few that survive and continue the reproduction of the species are those which —by special adaption for migration—reach a suitable spot for their growth. It does not necessarily follow that a plant producing a vast number of seed is more successful in establishing itself than one with few seed. It depends, rather, on the extent of vacant space suitable for its growth, and its facilities for dispersal. The most widely-dispersed flowering plant in the world, the common Reed (*Phragmites communis*) has the advantage of having a light plumed wind-dispersed seed, a rhizome which can be dispersed by water, and an adaptability for growth in both temperate and even Arctic regions and those of the tropics, in rivers, marshes and sandy shores, being suitable spots occurring almost all over the world. Damp soil is really all that it requires. Possessed of a rhizome throwing up numerous stems, it is able to form thickets so as to resist the encroachments of other plants. The number of seeds it produces is not large, nor is it, so far as is known, a plant of great antiquity.

Plants with wind-dispersed seeds have the advantage of rapidly and widely spreading seeds or spores. Hence the wide dispersal over continents, especially of *Compositae*, *Orchidaceae*, and *Ferns*.

Sea-dispersed plants have also a very wide dissemination on account of the large area of sea-coasts open to them. These, however, are mainly tropical plants, so that their area is more limited.

It is of some interest to note that the plant occupation of bare soil follows approximately the same order of settlers that was followed by the evolution of plants in the world, so far as we know it—that is to say, that Wind-borne and Water-borne seeds and spores come first, then those borne by Birds or Mammals, and that the lowest forms, cellular cryptogams, come first, followed by the higher forms. On a newly-built wall or the bare branch of a tree, in tropical countries, the first vegetation to appear are the algae, then mosses, then ferns, and finally the flowering plants, the Wind-borne seeds of orchids and plumed-fruited *Compositae* or plumed-seeded *Asclepiadaceae* being the first to appear.

In the Island of Krakatau, three years after the destruction of the flora by volcanic eruption, there were found, of wind-borne plants, spore plants 19, plumed and light seeds 5, sea-borne plants 6. Five species of orchids were found some years later, the minute wind-borne seeds of which, however, take some years to develop into plants, and they probably arrived as early as the spores of ferns. Plants whose seeds are borne by Birds did not appear till 14 years later, and then only 4, and 23 years later only 12.

The actual appearance of plants on new soil in most places, however, is influenced mainly by the character of the soil or surface, its humidity or dryness, and the kinds of plants in the vicinity, and is not necessarily a criterion of the amount and class of seed which falls on the spot. We know that there is in most countries a heavy, continuous rain of spores of *Algae*, *Fungi*, *Mosses* and *Ferns*, of which but few find a suitable habitat.

In Fernando de Noronha, a dry, almost xerophytic island, I could find only one Fern, five Mosses, and one Hepatic. In Christmas Island, 23 Ferns, 2 Lycopods, 15 Mosses, and 3 Hepatics. This difference was not, of course, due to any failure of dispersal in Fernando de Noronha, but to the fact that the environment (in this case the deficiency of rain-water) was unsuitable for

them, while the wetter climate of Christmas Island was suitable for these plants. The fall of spores which drifted in the air from Brazil was probably as great in Fernando de Noronha as from Java to Christmas Island.

Plants with More than One Method of Dispersal.

Some plants have the advantage of being disseminated by more than one method. In some cases two systems are combined. Thus the seeds of such plants as the Foxglove are blown by the wind, shaking the spike to some distance. When they fall, they are further carried from the plant by rain-wash. The Balsam (*Impatiens fulva*) has floating seeds. These are first thrown from the plant by explosion of the capsule, into a river, on the banks of which it grows, to be borne away and deposited on the banks, often a long distance from the parent plant. The seeds of *Impatiens parviflora* do not float. After their dispersal by explosion of the capsule, they may be washed a short distance by rain, but their spread is slower and shorter than that of *Impatiens fulva*. The seeds of fruit eaten by birds is deposited in the excreta on a post or rail, or branch of a tree, from which they are washed off by rain and often carried to some distance. The plumed seed of *Sonchus palustris* is blown by the wind, from the bank on which it grows, into the river, the plume becomes readily detached, and the achene (specially adapted for river-dispersal) is borne away until it is stranded on the mud by a falling tide.

Many of the most successful plants have facilities for being dispersed by several different methods, according to circumstances. The Shepherd's Purse, *Capsella Bursa-Pastoris* (*Cruciferae*), a native of Europe, now spreading over many parts of the temperate regions of the world, is primarily dispersed by the outer walls of the capsule being shed in dehiscence, and the seeds shaken off to a distance by the wind. They are also, when fallen, further dispersed by rain-wash, and are frequently carried about by man accidentally in soil and among other seeds, and by cattle eating the plant and passing the seed intact unharmed. It is due to the last two methods, which are of comparatively modern date, that it owes its wide distribution in Asia and America. There are many instances of this multiplication of methods of dispersal in the smaller herbaceous weeds; still, many plants which have but one adaptation for dispersal, if sufficiently effective, may be very widely distributed, provided that they find a sufficiently large area, or many small localities, in which they can grow successfully.

Origin of Modifications for Dispersal.

So far as I have been able to discover in cases in which we have a tolerably complete series of genera or species existing, there is no sudden change in Nature giving rise to modifications of fruit or seed for the purpose of dissemination. The evolution of a winged or adhesive fruit or seed seems to have been gradual, and to have been effected by a reduction or accrescence of certain parts, which had a primary use not connected with dispersal at all. The hairs, which are developed to protect an ovary exposed to rain from decay by the water resting on it in flower, may be further developed into wool in the fruit (*Anemone*), by which the achene is blown to a distance by the wind, or into stiff spines, or, further, into hooks for attachment to the fur of passing animals. In most flowers the sepals, whose original function is to protect the bud from injury by frost or rain, usually cease to grow after the opening of the flower, or freouently fall off, their work being done; but in the *Dipterocarps*,

for instance, they do not cease to grow, but continue persistent and growing till the fruit is ripe, and form wings for the flight of the seeds from the tree, or, as in *Isoptera*, form floating plates that the seed may be drifted far away along the streams and rivers.

Again, we have reduction of parts. Many plants have numerous ovules in the ovary, of which only one comes to maturity, or in plants with heads of flowers we find that, for Dispersal by Wind, only one flower in the head produces a seed. In these cases the unwanted ovules are abortive. Were they to be all developed, the whole of the seeds would germinate in a mass together, and perish from overcrowding. In Wind Dispersal it is essential that the seeds should be separated from each other.

In *Lunaria*, the Honesty, pods with four or five seeds are to be found on the plant, as well as those with only one, and the same thing occurs in some of the *Acacias*. The successful plants will be at length the 1-seeded ones. In the evolution of wings on a fruit from accrescence of the angles of the carpels, we find that this is also a gradual evolution, well shown in the genus *Combretum*.

The four angles of the fruit in some species are increased, so that, though not sufficiently enlarged to act as flying wings, they are really of use to the plant, for the fruit, when fallen, lying on two of the developed angles, is exposed above the surface of the ground to low air-currents, so that it is blown further along the ground than it would be if the body of the fruit was not raised a little above the ground. In other species these angles are formed into larger wings, and in others reduced from 4 to 2, giving a more distinct flight to the fruit. The accrescence of the angles is of use to the species from the beginning. These evolutions and modifications are described, so far as they can be detected, under the accounts of the various plants.

Evolutions of berries from capsules, due to a want of hardening and lignification of the walls of the pericarp, and of capsules from berries by the usually irregular and, as it were, accidental splitting of the enlarged pericarp, are also described in their place.

One of the most curious facts about modification for dispersal is that frequently the alteration so critical in the history of the distribution of a species is so minute and apparently trivial. The *Laburnum* pod usually dehisces and throws the seed out, so that it falls too close to the tree; it is not rare, however, to find that the funicle of a seed does not break on dehiscence and let the seed fall, but is somewhat firmer, and retains the seed attached to the valve till the valve itself, acting as a wing, is blown off to a distance from the tree, giving the seed a wider dispersal. It might happen in time that the seeds of this form alone would survive, and the *Laburnum* extend its range simply through the minutely greater toughness of the funicle.

Many of the sea-borne species of plants derive their vastly extended area of distribution entirely from a minute and inconspicuous space between the cotyledons, or between the seed and its testa, giving them buoyancy. The slightly thicker wings of the seed of *Dolichandrone Rheedii* convert the plant from a very local Wind-dispersed one to a species of a very wide Sea-distribution.

Again, the date of the dehiscence of a Leguminous pod (whether before its fall from the tree or after, or even when it does not ever dehisce) delaying the splitting of the valves till the fallen pod has decayed, may make the whole difference to the area which the species occupies, and to its success in the world.

These are only selections to show how small an alteration in structure or development of flower or fruit may permit a plant to occupy a much larger area in the world than it otherwise would, and to readily find a suitable spot for its further growth and development.

Overcrowding by Species.

In almost every plant the greater number of its seeds fall too near the mother-plant to be successful, and soon perish. Only the seeds which are removed to a distance are those that reproduce the species. Where too many plants of one species are grown together, they are very apt to be attacked by some pest, insect, or fungus. This is, of course, very well known to cultivators, whose plants in a limited area have to be carefully watched and guarded from disease. It is largely due to this also, in Nature, that one-plant associations are prevented and nullified by better means for the dispersal of the seeds. When plants are too close together, disease can spread from one to the other, and can become fatal to all. Where plants of one kind are separated by those of other kinds, the pest, even if present, cannot spread, and itself will die out, or at least become negligible.

In 1860 there were large plantations of Nutmegs in Penang and Singapore which were attacked by a small species of shot-borer beetle, destroying most of them. Estates were largely abandoned, and disappeared in secondary forest. I found many of the abandoned trees, in 1890, scattered through a mixed forest which had grown up between them. The insect had entirely disappeared, and the trees were healthy and thriving.

In " La grande Misère du chêne dans nos forêts Françaises " (*Rev. Eaux et Forêts*, lxv, i, 1927) J. Demorlaine imputes the gradual disappearance of the oak from French forests to stocking the forests purely with oak, and also to the repeated attacks of *Oidium* (*Microsphaera quercina*), as well as to caterpillar invasions. Thinning out these oak groves resulted in dying oaks acquiring new life in spite of attacks by fungus.

An island off Penang was covered with a forest of Mangrove, *Rhizophora*, *Bruguiera*, *Ceriops* and *Avicennia*. Owing to the demand for firewood, the plants of the first three genera were cut down and exterminated, *Avicennia*, useless for this purpose, was alone left. In 1897 the forest was attacked by the caterpillars of the moth *Hyblea puera*, and the foliage completely destroyed, to the great damage of the trees. *Avicennia* is very common, scattered through the Mangroves, but it does not get destroyed by this common moth, because it is protected by its being scattered through the forest, where the insect fails to find it. Many other instances of this could be adduced, in which the plants are protected in Nature by wide dispersal of their seeds. There are one-plant associations in the world which thrive either from want of competition with other plants, or due to exceptional circumstances; but they are in many cases of not long duration, and usually are at last thinned out and replaced by other plants, after the attacks of one or other pest.

Change of Vegetation.

An exposed bare land surface, unless quite unsuited for plant growth such as a desert, shifting sandhills, or dry soilless rocks, is soon covered with an invading vegetation, and eventually may be so thickly covered that there is no space for other invaders. Seeds then falling on the ground either do not germinate, or fail to reach maturity. In forests they are unable to obtain sufficient light from the dense overshadowing canopy of foliage; in open downs they fail for want of root room, and probably from insufficient water-supply. Such spots, which are as heavily covered with plants as is possible, may remain unaltered, as regards their flora, for many centuries; but here and there plants die out, and the nearest seed on the ground may have its opportunity of growth. On the Downs and in the Forest there is a constant

fall of seed waiting its opportunity for the death of a plant, or the fall of a big tree attacked by fungus, struck by lightning, or thrown down by the wind, and the first seeds on the spot secure the place. For every empty space there are numerous competitors. Besides the openings due to the natural death of plants, there are other constant changes taking place. Denudation is continuous throughout the world, shifting of soil by rain-wash, flood and river. A forest stream, blocked suddenly by a rock fall, may alter its course and deposit its silt on a meadow, or in a forest edge, or seashore, destroying and altering indirectly the existing flora. It may even make a lake in a portion of a valley or lowland district, destroying the forest which formerly occupied it, so that the area, formerly a dense forest, may become a marsh or pond with aquatics brought by wandering wild-fowl. This lake, in turn, may at length be silted up, and first marsh plants, then forest, will cover the ground again.

These changes of vegetation are constantly, and in most countries continuously, going on, and, accompanied by changes of temperature and rainfall, action of man, etc., are responsible for the change of vegetation. The plants which have the best means of dispersal of seed will be ever the conquering invaders of new ground.

It is quite clear that in many instances, especially in the case of trees, a large number of specimens cannot grow close together. Indeed, in tropical forests large trees of one species are usually 30 feet apart. But in smaller trees, and even shrubs and herbs, the same kind is usually separated by some distance from the mother-plant. Many-seeded plants frequently drop their seeds on the ground in a small space; they germinate, but in a very short time all perish. I have elsewhere detailed the account of the spread of *Digitalis* in New Zealand, where, while one farmer, ordered to exterminate the plants on the ground (it being considered a pestilent weed), dug up all he could find, thereby clearing away all the visible young plants, and was never free from the pest, another left them as they were, and the plants practically killed each other, and the pest disappeared altogether. A Sycamore tree (*Acer pseudoplatanus*) in my garden sheds annually a large number of seeds, of which a large proportion fall at the base of the tree or within its shadow. They germinate, and all perish within the first year. The only offsprings of the tree which survive and develop are those that are blown by the wind to a distance of some yards from the tree, and fall far apart from each other. A tree of *Heritiera elata* (*Sterculiaceae*) in the forest of the Botanic Gardens, Singapore, shed a very large number of fruits, which fell all round the tree. Hundreds of these germinated and grew for a little. Next year the number had largely diminished, till in three or four years hardly one had survived.

Indeed, it may be said that of the vast amount of seeds produced by any plant, far the greater number perish; only those survive and develop into plants, and continue their race, which find a suitable spot to grow in, and this is effected by their various modifications for dispersal.

Endemics and Epibiotics.

While some plants are widely distributed over areas of large size, and often abundant in their area, every country contains some that are rare, and some which are limited to a very small area, and not to be found elsewhere in the world. These latter have constantly been known as *Endemic* plants; but as they are thus limited by one of two distinct causes, the name *Endemic* is reserved for those which are related to, or evolved from, other plants in the same area, or, in an oceanic island, evolved or modified sufficiently to be

considered distinct from another species which formerly invaded the island. A number of these plants of limited area, however, are the relics of an earlier flora which has nearly disappeared from change of climate or environment. These are known as *Epibiotics*, or survivors. If circumstances permit, Endemics may spread and become ordinary widespread successful plants. They are comparatively new-born species. Epibiotics, on the other hand, are at the end of their species life. They do not spread. Remains of a flora which had long disappeared, they persist only in an isolated spot which, for some reason, has not been overwhelmed by the later invading flora, but are unable to spread any further. They are usually unprovided with sufficient means of dispersal to cross the barrier of the modern flora, and to reach another suitable spot for their growth.

There was an attempt made, in Willis's " Age and Area," to show that the widely-distributed plants of the world were the oldest evolved, and the Endemics (including Epibiotics) were the latest evolved. Naturally one would think that the oldest species, having had more time to spread over the world, would be the most widely dispersed and most abundant species. But this has been shown not to be the case. The most widely-dispersed plants are those which have the best means of seed dispersal, and which possess the greatest adaptability for various climates and environments. Many plants, which at one time were widely dispersed owing to changes in their surroundings, became scarce, then Epibiotic, then perhaps disappeared entirely. I give an illustrative case of this. In the Malay Peninsula there is a small genus of *Gesneraceae*, *Loxocarpus*. The plants grow on damp or wet rocks in forest, and possess a capsule containing minute seeds dispersed by rain-wash from rock to rock only. The species are scattered over the Peninsula, but usually very locally, and often at long distances apart. In a dense forest in Negri Sembilan I came to a few large blocks of rock projecting from the deep mass of soil and dead leaves which had engulfed the underlying rocks. On these blocks was a very small species of *Loxocarpus*, and it was limited to one or two of the projecting portions. The little plants produced plenty of seed, but to no purpose for dispersal; washed off the rocks by the rain, they could only be deposited on the deep soil below, where they could not possibly grow. This little plant was, doubtless, a survivor from the time before the forest, growing over the granite rocks, had covered them with this deep carpet of soil, when the *Loxocarpi* were abundant all over this mountain region. Now it still remained isolated on its rock, and would, perhaps, so remain till the rise of the forest-floor covered the rock, when it would become extinct. Here is a species dying out, not from any change of climate, but from a slow change in its environment, unable to adapt itself to the change, and possessing no adequate means of dispersal to enable it to cross the rising tide of the forest-floor to other rocks. There are very many similar instances all over the world. The continental islands, Canaries and Madeira, Mascarene Islands, Socotra, etc., all retain the remains of floras now long disappeared from the lands to which they were formerly attached.

Evidence of Land Changes Based on Dispersal.

The study of dispersal methods assists very considerably in the explanation of the causes of the distribution of plants, not only in the obvious ways in which plants have migrated directly by Wind, Water, or Animal transport, but in many cases it may indicate a former connection of land between two (now sea-separated) countries.

In Selangor, at an altitude of about 4,000 feet, in the midst of tropical forest, I came across a spot on which were growing together *Viola serpens*, *Sanicula*

europaea, *Desmodium scalpe*, *Disporum pullum*, *Didymocarpus albinus*. These plants were confined to this spot, and do not occur elsewhere in the Peninsula, so far as is known. They are of a Palaearctic Himalayan type of flora, scarcely represented at all in the Malay Peninsula, but occurring in Java. I was puzzled to account for their presence here, till later I visited the Battak country, in Sumatra, opposite the locality of Telom, in Selangor, where I found them. Here I found all of these plants growing together at a height of 4,000 to 5,000 feet altitude, and much more abundant. The two localities are separated by 250 miles, of which about 150 is sea. Now, of these plants the *Disporum* has berries, and might have been brought by birds, *Sanicula* has adhesive fruits only, transported by mammals, and the others can only be dispersed by rain-wash. In fact, only the *Disporum* could possibly cross the sea. It is therefore quite clear that at one period there must have been a land connection between Berastagi in Sumatra and Telom in Selangor, at the height of 4,000 or 5,000 feet, otherwise it would be impossible for these plants to have got to the two places.

The flora of Gunong Tahan, in the Malay Peninsula, contains a number of plants only known elsewhere in Mount Kinabalu, in Borneo, mostly small-seeded plants, *Eriocaulon*, *Scirpus* and other *Cyperaceae*, *Gentian*, etc. The distance between the two localities at the present day is over 1,000 miles, mostly sea. It is quite impossible for the seeds of these little plants to have been blown across this great distance, and we can only conclude (a conclusion confirmed by other evidence) that there was at one time a direct land connection between the two spots.

What kinds of plants can cross the sea we know by reference to island floras. When we get a single species of plant, only occurring at two spots far distant, we may be a little doubtful as to this proving a former land connection between the two spots, but when we find several species together in both localities, it may be considered as certain that the two floras have been at one time continuous. Of course the human element must be excluded, but this is easy, as we know the class of plant conveyed by the human race, and usually have other evidence of previous human settlement.

Effects of Dispersal on Distribution.

When we look at what is known as the distribution of a species or genus throughout the world, we find that a common or world-wide plant mainly owes its extensive area of habitation to certain facilities for distribution in some way, although at the same time each plant has its limit. Many plants, with apparently excellent adaptations for migration, do not occur in areas which their seeds or spores could easily reach, and which in many cases they do reach. This is due to their limitations in environment in many cases, their exigencies in soil, climate, or in one of the numerous factors which are necessary for the plant in order that it may grow and propagate itself successfully in any given spot. The more specialised a plant is, the larger will be the number of concomitant environmental factors it will require, and the more limited will be its area. The simplest plants, the cellular Cryptogams, are the most widely distributed. The *Myxomycetes* that we find in damp spots in England are nearly all species found equally widely in the tropics. The fact that their spores are very readily dispersed by wind is, of course, an important factor in their wide distribution, but is not the only cause of it. The exigencies of their life-history are small, and the localities suitable for their development are abundant in all parts of the world. Their early evolution in the world's history, and consequent antiquity, has little or nothing to do with the wide distribution of species.

It was formerly common to describe genera, and more especially species, which were scattered all over the world as cosmopolitan; but a large number of flowering plants so described by the earlier botanists owe their wide distribution merely to the recent actions of man, and so their "cosmopolity" may be considered artificial. This class of plants must be clearly distinguished from those which have migrated across the world, retaining their original characteristics, and successfully established themselves, so that, independent of any aid from man, they have managed to become constituents of the floras of many countries.

Our system of arranging plants in orders, genera, and species, and separating one from the other, is to some extent artificial, and varies often according to the ideas of different botanists. A truly cosmopolitan plant is one which has travelled by natural methods to all parts of the world, and in so doing has not altered its characteristics sufficiently to be classed as a distinct species by botanists.

The number of orders common to the greater part of the world is large, the number of genera (in proportion to the large number of genera recognised by botanists) smaller, and the number of species very small. I here refer to flowering plants and vascular Cryptogams only. As we descend to the lowest plants, the cellular Cryptogams, we find more and more are cosmopolitan.

I do not intend in this work to attempt to give any account of the *distribution*—that is, the localisation—or of the *limits* in area imposed by Nature on species of plants, as that belongs to a different subject. I merely treat of the main *cause* of distribution of plants throughout the world—that is to say, *Dispersal*. I treat of the various methods of dispersal in the order in which they were evolved in the history of the World, viz., by Wind, Water, Animals and Man, adding at the end various minor methods, such as explosive mechanisms and spread by creeping rhizomes, etc.

HENRY N. RIDLEY.

CHAPTER I

DISPERSAL BY WIND

PART I

Foreword—Dust and Stones borne long distances by Wind. Wind Force—Seeds and Fruits blown along Ice—Methods of Dissemination by Wind.

THE wind plays one of the most important parts in the dissemination of plants, not only in scattering far from the parent plant such seeds, or one-seeded fruits, as have some special modification such as wings or plumes, but very largely those of which the small size and lightness are the only aids to dispersal which they possess.

There are few times when, or places in which, the wind is not sufficiently strong to drift along some of the best furnished seeds at least. The greatest general effects are produced in open country, in steppes, open heaths or downs, deserts, sand dunes, and along the borders of woods and forests, river banks and roadsides, and it is in these localities that we usually find the greatest number of plants whose seeds are furnished with flying apparatus.

In the thick forest there are far fewer, as the wind is often not strong enough near the ground to carry plumed or winged seeds along, though the slightest current of air there, is sufficient to waft away the very light seeds of ground orchids and the spores of ferns. But many of the lofty trees, exposed at the top to the strong gales, possess winged or plumed fruits, and many epiphytes on their highest branches, *Orchidaceae*, *Bromeliaceae*, *Aeschynanthus* (*Gesneraceae*) *Asclepiadaceae*, have modifications for flight of the seeds.

In open country, when the wind is comparatively light, and progresses by waves, the plumed seed is carried rapidly at first, then slower, till it drops, then a second blast may pick it up again and carry it further, and so it may go on for a long distance till it is stopped by some obstacle, or, because too wet to fly further, it remains on the ground, which is the reason why we see abundance of plants, such as dandelions and groundsel and *Poa annua*, so dispersed, along the bases of walls. The upper layers of wind currents are often, however, continuous, as can be seen by the movement of the clouds in a gale, and though I doubt if the seeds of most flowering plants, even if plumed, could rise to this height, spores and the minute seeds of orchids could easily be thus carried. However, the long distances to which plumed fruits of *Compositae* and seeds of *Asclepiadaceae* are carried across the sea (as will be shown later) seems to suggest that they have been carried by a continuous wind current. Investigations on the altitude to which seeds and spores can be carried by wind might well be carried out by aeroplanes, but I have found that few experiments made of this nature are recorded.

DUST AND STONES BORNE LONG DISTANCES BY WIND. WIND FORCE.

As many small seeds, as well as the spores of ferns, fungi and algae, are much lighter than dust or small stones which are borne to a great distance by wind, it becomes necessary to see how powerful the wind can be in lifting small objects and conveying them afar.

Darwin (" Voyage of the *Beagle*," chap. i, p. 5, ed. ii.) gives several instances of the fall of dust on ships at long distances from land. Samples of dust which fell a few hundred miles north of Porto Praya, Cape Verde Isles, sent by Lyell, consisted largely of infusoria with siliceous tissue of plants. He records no seeds in the dust, but mentions finding, in dust collected 300 miles from land, particles of stone above a thousandth of an inch square. The wind that carried these particles could certainly carry fern spores and seeds of orchids and possibly some of the lighter seeds of other plants. It is well known that in the Canary Isles, 50 miles from the African coast, the hurricanes frequently bring clouds of dust from the African desert, and these might bring also very small seeds. A. R. Wallace (in " Darwinism," p. 363) gives some data supplied to him by Professor Judd on the dispersal of dust. Some which fell at Genoa in October, 1885, was believed to have come from the African desert, about 600 miles; some of the particles of quartz, hornblende, and other minerals had a diameter of $\frac{1}{200}$ inch and weighed $\frac{1}{200000}$ of a grain. The dust from Krakatau fell on the ship *Arabella* 970 miles from the volcano, particles of which were $\frac{1}{200}$ inch through, and those which fell at Batavia, 100 miles away, were $\frac{1}{50}$ inch long and $\frac{1}{70}$ inch through. Sir John Murray, of the *Challenger* Expedition, informed him that he found in the deep-sea deposits, rounded particles of quartz $\frac{1}{250}$ inch through, 500 and even 700 miles west of the African coasts and at equally great distances from Australia. He considered them to be atmospheric dust carried that far by the wind. This is less satisfactory as evidence than the fall of dust at Genoa and from Krakatau, as the deep-sea dust might be derived from floating timber, ships, etc. These grains of dust, however, are very much lighter than any seeds of flowering plants, though, as Wallace says, the seeds of many plants are flattened, and so expose a larger surface to the wind, and would fall at a slower rate than the quartz sand. Wallace points out the difficulty of detecting a fallen seed small enough to be carried by wind to any distance. This is a difficulty undoubtedly, but we can judge by the distribution of plants how far the small-seeded plants can go, especially by examining the floras of distant islands where any seeds borne by wind must have been carried across at a flight.

Estimating the specific gravity of quartz at 2·6, Wallace finds that the particles of quartz found by Murray 500 to 700 miles from land would weigh $\frac{1}{25000}$ of a grain each, and the Genoa dust, which was carried probably over 600 miles, weighed $\frac{1}{200000}$ of a grain.

P. A. Buxton (in " Animal Life in the Deserts ") gives a graphic account of the violence of the wind in these regions. He quotes Angieras, who was kept prisoner by wind under a rock in the Western Sahara for nine days in 1915, and some months later experienced a gale which carried a camel saddle for 200 metres (over 600 yards).

Whirlwinds, which can carry seeds or fruits to a considerable distance and height, seem to occur frequently in the desert. Lane measured one which was 750 feet high, and saw others even taller. Flying officers in Mesopotamia encountered vortices whirling upwards at a height of 5,000 feet above the ground, still carrying dust and debris. In 1918 a camp was struck

by a dust-devil at Balad Ruz, north-east of Bagdad, in which heavy articles of kit were blown 200 yards through the air, and an officer was scooped out of his tent with all his camp furniture and dropped twice, the second time with several broken ribs.

Lyell (in the " Principles of Geology ") describes the eruption of Tombaro in Sumbawa Island in 1815, when violent whirlwinds carried men, horses and cattle into the air; and the ashes were carried to Java (300 miles), Celebes (217 miles), and to Amboyna and Banda (800 miles). These ashes were very fine, however—in fact, described as an impalpable dust. He also mentions a shower of ashes from Coseguina, in Mexico, falling in Kingston, Jamaica, about 700 miles away, which travelled for four days at a rate of 170 miles a day.

There are other records of the great distance to which volcanic ash can be carried by the upper wind currents. The ash is, however, very fine and light in these cases, though probably not lighter than spores of ferns and fungi, and possibly in some cases not lighter than the seeds of orchids.

G. Beauverd (in " Quelques cas de dissemination des graines par le vent," *Bull. Herb. Boiss.* 1901, p. 633) writes, that being in Bas Valais in July, there was a north-west gale of great power, during which an immense mass (plaque) of snow was blown over his head from a cornice, carrying with it a quantity of earth and debris of plants. He noticed that the snow on Les Cornettes was full of dead leaves and samaras of maple, the nearest trees of which were 4 kilometres (3·16 miles) away, about 1,000 metres lower. In another July storm in Valais he saw boughs of fruit trees carried to great heights, and also saw ears of corn which had been brought by wind at least 3 kilometres, and branches and seeds of elms carried to great distances.

Vogler (in *Flora* 89, " Über der Verbreitungs-mittel der Schweizerischen Alpen-pflanzen ") estimated that seeds during storms in the Alps might be carried to a distance of 20 kilometres (12½ miles), and cites a remarkable hail of salt on the St. Gothard on August 30, 1870, when crystals of salt weighing in some cases 0·76 grammes (10·6 grains) fell, which had been blown from North Africa or the nearest sea coasts, at least 156 miles; and Rollier describes a rain of stones, white quartz pebbles as large as peas and hazel nuts, presumably from Southern France or Spain, at Trelex (Vaud) on February 20, 1907, from a distance of more than 62 miles.

J. Rouget and Davy de Verville (in " La tempête du mois de décembre 1925, et l'aeronautique vegetal," *Rev. Gen. Bot.* 39 (454), p. 545 (1926)) give some account of the results of this storm. After it was over they found in profusion fruits and seeds of *Tilia platyphylla* and *T. sylvestris* with those of *Alder*, *Birch*, *Ash*, *Acer pseudoplatanus* and *A. platanoides*, *Abies pectinata*, *Picea excelsa*, *Pinus sylvestris*, *P. laricio*, *P. maritima*, *Clematis*, *Composites*, *Epilobium*, *Eriophorum*, *Platanus*, *Robinia pseudacacia*. As most of these plants grew at no great distance in the vicinity, it was not possible to discover from whence most of them had come, but the nearest fruiting plants of *Abies pectinata* were 7 or 8 kilometres distant, and they estimate that the distance the seeds must have come was at least 12 kilometres (about 8 miles). They noted that the seeds or fruits of one kind more or less fell together, at one spot *Tilia*, at another Birch. This I presume is due to the different weights of the fruits entailing a kind of sorting in falling.

Warming records, in his writings on the floras of the northern regions of Europe, that large quantities of plant debris, mostly fruits of *Calluna vulgaris* mixed with blossoms of *Erica tetralix*, were, during a gale in February, 1881, blown across the Cattegat from the Swedish coast to the eastern shores of Jutland, a distance of 110 to 120 kilometres.

In sandy deserts and sand dunes, seeds, fruits, and sometimes bulbils or even whole plants (tumble-weeds) are blown along until they come to rest on

reaching a depression in the sand or some other obstacle. In these depressions the sand is stationary, the sunken surface not having being exposed to the wind, and they thus become a suitable place of growth for the seedlings, which cannot grow in constantly shifting sand. In the deserts of Helouan in Egypt and of Bikanir in India I observed that most of the plants grew in depressions formed by subterranean streams or springs, which spots were slightly damper and the soil firmer than in the surrounding deserts. The seeds or fruits were blown along over the deserts till they reached one of these depressions, where they rested. Shrubby plants, thus brought to the spot, developed and formed thickets which delayed the flying seeds and fruits of herbs, and thus the greater part of the flora was to be seen in these depressions. In fact, these wadys, where in the rainy season the streams run, and the damp depressions, where in Bikanir the underground water comes near the surface, are distinguishable a long way off by the vegetation.

I noted in Helouan in these damp spots the following plants, all with small seeds or fruits blown along by the wind to their resting-place: *Farsetia aegyptiaca*, *Zilla myagroides*, *Diplotaxis acris* (*Cruciferae*), *Reseda pruinosa*, *Trigonella anguina*, *Scrophularia deserti* and *Cynodon dactylon* (*Gramineae*).

H. Hamshaw Thomas (in " Some Observations on Plants in the Libyan Desert," *Journ. Ecol.* 1921, p. 87) describes thus the dispersal of *Calligonum comosum* (*Polygonaceae*) :—

" The fruit is covered with short, spiny processes, red or yellow. These " fruits are dispersed by the wind, the spiny processes rendering them more " bulky without contributing much weight. During the sandstorms of April " the fruits were seen rolling along the sand in all directions at a rapid rate, " and some found their way into tents or came to rest in sheltered spots under " other plants. There can be little doubt that the means of dispersal is an " efficient one, and is the cause of solitary specimens in the desert far from " other plants."

The processes in such cases have two functions, firstly, on the shifting sand exposed to the wind they raise the fruit above the surface and so expose it to the wind (one can compare with this the evolution of flying wings in the winged fruits where the angles of the carpels are enlarged, so that the fruit does not rest flat on the ground, but is elevated, which allows of the fruit being rolled over and over by the wind, as in *Halesia*), and secondly, the processes act as anchors when the fruit comes to rest in a firmer (and in the deserts, damper) soil.

Jean Massart (in " Voyage botanique au Sahara," p. 322) writes as follows :

" The wind is undoubtedly the chief agent of dissemination (in the desert). " Let us record some types in which the organs of transport are specially " developed. *Ephedra alata*, of which the seeds are surrounded by scarious " bracts ; *Aristida*, the fruit of which is surmounted by a long awn, trifid " and plumed, depending from the lower glume ; *Salsolas*, *Haloxylon articulatum*, " *Noaea spinosissima*, of which the winged calyx forms a parachute to the fruit ; " *Calligonum comosum*, whose fruit is provided with long red (rousses) branched " processes ; the *Farsetias* and *Henophyton deserti*, whose flat seeds are sur- " rounded by a large white wing ; *Zilla macroptera*, which has indehiscent silicules " provided with 4 longitudinal wings ;. *Cleome arabica* with globular seeds, " long velvety ; *Erodium* and *Monsonia nivea* with their long silky awns ; *Tamarix* " and *Daemia cordata* with plumed seeds ; *Anthyllis sericea*, of which the pod " is enclosed in the balloon-like calyx, and *Marrubium deserti*, its calyx, instead " of having hooks or points which exist in most species, having the limb " widely spread out in the form of a parachute."

On the chalk downs in Dorsetshire and other southern English counties, throughout the greater part of the year, the wind blows in light puffs strong enough to scatter minute seeds or fruits, even of quite low-growing plants; but many of these have the stalks of the fruit-heads 6 inches or more tall, and during the winter months, when much of the foliage is withered and the fruit-heads more fully exposed to the blasts, and the winds are more violent and persistent, the dispersal of these seeds and fruits must be much more extensive.

Characteristic plants in these localities which I have seen to be wind-dispersed are *Poterium sanguisorba*, the one-seeded fruits of which are readily blown to some yards distance; *Plantago lanceolata*, *Linaria minor*, *Draba verna*, all of which have small light seeds; many grasses, some helped by their persistent glumes acting as wings; *Ophrys apifera*, *Orchis pyramidalis*, *O. ustulata*, besides the plume-seeds of thistles, *Hieracium pilosella*, *Crepis virens*, *Hypochaeris*, etc.

In close-turfed spots like this, the rainfall (though it must be taken into account) can act but little as a seed-disperser, for the small seeds blown from the herbs as they fall to the ground are caught in the herbage and there retained. In a spot on the Swanage downs where the turf had been removed some time previously, the whole bared earth was scattered over with seedling plants of *Poterium sanguisorba*, *Plantago lanceolata*, a few thistles, and *Hieracium pilosella*. Some of these seeds may have fallen previously and remained dormant beneath the soil and turf, and only germinated when they were exposed to the air by removal of the turf—for it is well known that many seeds when buried can retain their vitality under the soil for some years—but they appeared to have been largely blown from the adjacent downs upon the exposed soil.

Vogler (*Flora*, Bd. 89 (1901), p. 71) gives a long account of the dispersal of seeds in the Swiss Alps, and specially an account of the plants found on ground exposed by retreating glaciers. He showed that about 25 per cent. of these plants thus found were wind-carried or could be wind-carried, including among them those with hairy or winged seeds or fruits, and those with very small seeds. I cannot see that he anywhere allows for rain-wash, which may also have taken part in this dispersal, but undoubtedly wind has effected to a great extent this re-covering of exposed soil.

In the same paper Vogler gives some accounts of the occurrence of wind-borne leaves to long distances in the Alps, the observations being made by Messrs. Coaz, Christ, and Muret. The importance of these observations lies in the weight of the substances which can be carried far by wind, and also, as pointed out elsewhere (and it must be taken into account) that it is possible for leaves blown long distances to carry with them seeds accidentally attached (especially such seeds as have mucilaginous testas). I have frequently observed that dry fallen leaves fly in storms further than winged fruits or seeds, and that those which rise most easily from the ground and are carried furthest are those that are partly bent by drying and so expose a greater surface to the wind. Coaz found Beech leaves blown on to glaciers at a distance of from 5 to 11 kilometres (approximately 3¼ to 7 miles), and Chestnut leaves at a distance of 12 kilometres from the nearest trees. Christ found Beech leaves blown 15 kilometres, and Muret found the leaves of *Pyrus* (*Sorbus*) *aria* at a distance of from 15 to 20 kilometres (about 14 miles).

On the Scotch mountains the winds sweep with great violence in strong blasts, often producing small whirlwinds, carrying before them the water of the streams as fine spray, and even blowing away pieces of the turf, with sticks, leaves, etc., for several hundred yards. Most of the Alpine plants have very fine and small seeds or fruits, and these could easily be carried by a succession of blasts for a considerable distance. Characteristic types of these plants are *Thalictrum alpinum*, *Saxifragas* of several species, *Alchemilla alpina*,

Cherleria sedoides, *Silene acaulis*, *Gentiana*, *Azalea procumbens*, *Sibbaldia*, *Potentilla*, *Junci*, *Carices* and grasses, besides plants with plumed seeds or fruits, *Saussurea*, *Hieracium*, *Taraxacum*, *Crepis*, *Mulgedium* with plumed fruits, and *Epilobium* with plumed seeds.

The winds blow from the heights up or down the valleys in every direction, and when violent could easily carry the seeds across from one mountain to another.

Rain-wash and streams play their part in distributing some of the smaller seeded plants like *Veronica*, *Sagina*, *Chrysosplenium*, *Pinguicula*, and *Saxifraga aizoon*, as well as many of the plants referred to above, but it seems clear that most of the former are at least mainly dispersed by wind.

In open woods, downs, deserts and open spaces generally, the action of the wind in disseminating seeds is very considerable, as even a comparatively light wind will carry seeds of some weight for a considerable distance. The strongest winds in Europe usually blow in the autumn and winter, when most plants are in fruit, and should any fruit remain on the plants through the winter, it is scattered by the strong winds of March and April. Thus I have seen the fruits of *Ilex*, *Viburnum Tinus* and *Crataegus* rolled along the ground for some distance in March, and at the same time the heads of fruit of *Platanus* break up and the plumed seeds are borne as far as 150 yards from the tree. The distance to which the various classes of wind-borne seeds can be carried by a wind of ordinary strength will be discussed under their several headings, but attention must be paid to exceptional bursts of wind, such as occur frequently in cyclones, typhoons, or whirlwinds in all parts of the world.

The Rev. E. A. Woodruffe-Peacock (*Selborne Magazine*, xxviii, 40) gives some account of " dispersal " by what he calls " storm-columns," which he distinguishes from " whirlwinds " by the greater distance covered or affected by them, the latter shifting material and seeds from a few yards up to 150 yards, while the former carry material for a distance of 25 miles at least. I do not think that there is any necessity to separate these two classes of whirlwinds merely on account of the distance they cover, or the amount of air implicated in the whirlwind.

In England these whirlwinds usually occur and are seen in the hot summer weather of July and August. The heated air from the ground ascends and, meeting and mixing with the upper descending currents of cool air, forms a spiral twist, lifting sand, leaves, hay or any light material and causing it to ascend to a very considerable height, about 100 feet or even more, according to the size of the whirlwind. I have seen them twice in two years in the same hayfield at Bishopstone in Herefordshire. The hay had been cut, and a cartload was standing when the whirlwind struck it and carried the whole contents of the cart to a height of about 100 feet. The contents moved fairly fast for some distance before the heavier fragments began to fall, and I estimate that it must have been carried nearly 2 miles before most of it had fallen, as I travelled that distance for the purpose of observation.

Woodruffe-Peacock describes a similar occurrence in a hayfield, stating that about two wagon-loads of hay were gathered up by a whirlwind for a distance of about 40 yards of its track. He also describes seeing a fall of cut hay on the road between Ilford and Barkingside in Essex during a very gentle south-west breeze, and gives a list of the plants he detected actually falling. These were: *Agrostis vulgaris*, *Alopecurus pratensis*, *Anthoxanthum odoratum*, *Arrhenatherum avenaceum*, *Briza media*, *Bromus mollis*, *Cerastium vulgatum*, *Holcus lanatus*, *Lolium perenne*, *Poa pratensis*, *Stellaria media*, *Taraxacum officinale*, *Trisetum pratense*.

At Cadney (Lincolnshire) in August, 1897, he saw the result of a whirlwind which must have taken place in the night or early morning. The fall of plants

very thinly covered the whole parish, 5,000 acres, and extended still wider. It contained sand-dune plants from at least 20 to 25 miles distance, viz., *Spergularia neglecta*, *Ononis repens*, *Allium vineale* and the glaucous seaside form of *Agropyron repens*. All these were plants torn up by their roots. There was also a rooted plant of *Vicia cracca* and a quantity of cut meadow grass. At the same spot, in July, 1908, he saw a similar shower of cut grass and uprooted plants, but covering a smaller area. Among the uprooted plants were *Koeleria gracilis*, *Avena pratensis* and *Hippocrepis comosa*, the origin of which he traced from the limestone of the cliff range of hills. Besides the plants mentioned above as occurring in these whirlwind falls, he adds in his list: *Achillaea millefolium*, *Anthriscus sylvestris*, *Avena pubescens*, *Capsella Bursa-pastoris* (rooted), *Cynosurus cristatus*, *Dactylis glomerata*, *Deschampsia caespitosa*, *Festuca rubra* (rooted), *Festuca ovina* (rooted), *Leontodon autumnalis*, *Lotus corniculatus* (rooted) and the fleshy sea form *crassifolius*, *Poa trivialis*, *Rhinanthus Crista-galli*, and *Rumex acetosella*.

Except such seeds as were still in the panicles or racemes of the fallen grasses, he saw no seeds falling, which, indeed, would not be easy to detect. Nevertheless, seeds and small fruits must often be carried up and scattered over the country by these whirlwinds, but—as he suggests—owing to their greater weight they would probably fall sooner than the light culms and branches of herbs.

I have already mentioned the more violent whirlwinds or " dust-devils " of Africa and Mesopotamia, which are able to carry fairly heavy seeds a considerable distance. Cyclonic wind-storms frequently occur in the tropics, and I have seen several in the Malay Peninsula. They do not occur in hot or dry periods, but frequently on rainy days, and are often accompanied by rain-storms. They appear suddenly, apparently swooping down from the sky to the ground with great violence, twisting round the trees in their course, tearing them out of the ground and wrenching off the branches. They often cause great destruction in the forests, cutting lines of a quarter of a mile or more through them, and throwing down gigantic trees. Moving with great rapidity for half a mile or more, they rise and disperse. I have never seen boughs and other material carried by them to a greater distance than from 12 to 20 yards, nor carried to any height.

The typhoons of the Chinese regions and elsewhere may in some cases carry seeds to a considerable distance, but I have no record of their being a means of dispersal.

In dense tropical forests the wind has much less effect than in open country, as it can only act upon the uppermost branches of the tree canopy. The low terrestrial herbaceous plants, herbs and shrubs are practically unaffected, even when a hurricane is ranging among the tree tops.

I was on one occasion in the Pahang forests, in the Malay Peninsula, when a violent " wind-storm " struck the jungle. The trees formed a canopy above, about 150 to 180 feet from the ground, so dense that I could not perceive any wind below, where I was standing, though huge boughs of trees and large pieces of decayed wood were falling round me in every direction, and there was a continuous roar in the tops of the trees. Storms like this usually last only a quarter of an hour or so, and may easily whirl seeds of epiphytic plants on the upper branches, or the winged fruits of the trees themselves, to a considerable distance.

The stillness of the air at the ground level of the forest accounts in great measure for the absence of the plume-fruited *Compositae* and the plume-seeded *Asclepiadeae* and most of the *Apocynaceae*, as well as the light-fruited grasses and plants with capsules of small seeds, or light one-seeded fruits such as the *Rubiaceae*, *Hedyotis*, *Oldenlandia*, *Borreria*, *Spermacoce*, *Cruciferae*, *Labiatae*,

Scrophulariaceae, etc., many of which are abundant on the open cultivated lands outside the forests. These seeds, if blown towards the forest, are stopped at the edge by the dense mass of stems and foliage fringing the jungle.

The lalang grass, *Imperata cylindrica*, with its plumed spikelets, seems quite unable to traverse even a short belt of forest of about 30 yards thickness. The usual flight distance of the fruit from the level of the top of the plant appears to be about 16 yards, but from hill tops over open country it could doubtless fly farther, and it reached Krakatau after the eruption fairly early. If, however, roads sufficiently wide are made through the forest, it can drift up these, but quite a narrow band of vegetation stops its flight.

In the same way thistles and many plume-seeded plants like *Epilobium angustifolium* in England only occur in the thicker woods when the woods have been cleared in patches. This class of plant, however, readily passes up through forest or dense woods where paths have been cut, or where rivers go, as there are always air-currents passing through either way, as is shown by the large percentage of *Compositae*, Willows, and other plants with plumed fruit or seeds occurring along river banks or woodland paths, and in this way they may migrate through forest to open country or hillsides beyond. The migration here is assisted, however, along forest paths by other causes, viz., the passage of cattle, human beings, and wild beasts, which, feeding on the grasses and small herbs, evacuate the seeds as they pass on, or carry the fruits attached to their feet, hair or clothing.

The greater number of the capsular herbaceous plants of the dense forests, such as *Ophiorrhiza*, *Argostemma*, *Pomazota*, and the *Gardeniella* section of *Gardenia* (*Rubiaceae*), the *Didymocarpi* and their allies (*Gesneraceae*), *Sonerila* (*Melastomaceae*), seem to rely mainly on "rain-wash" as the agent for their dispersal.

Grasses, except Bamboos, are remarkably rare in the forests, being represented mainly by species in which the glumes or spikelets are armed with adhesive processes, such as *Centotheca*, *Lophatherum*, *Streptogyne*, and *Leptaspis*, all dispersed by attachment to the fur of passing animals, and *Cyperaceae* in the Malay forests mainly by *Mapania*, the large nuts of which are probably dispersed by rats. In the *Labiatae* the *Gomphostemmas* have white, fleshy nucules, and *Hedyotis congesta* (*Rubiaceae*) has the capsule—white and fleshy—dispersed by birds. These curious modifications of plants (whose seed in the remaining species of their genera is mainly wind-dispersed, with the complete absence in the forest of the typical forms) illustrate the impossibility of adequate wind-dispersal, at ground level in the dense rain forests of the Equatorial regions, of seeds heavier than those of the orchids.

There are, however, light currents of air along the ground through the forests which will carry spores of ferns and Selaginellas, as well as those of Mosses, Hepatics, and Fungi, and the light seeds of terrestrial orchids, *Burmanniaceae*, *Triurideae*, and *Balanophora*, as well as some, at least, of the *Begonias*. The terrestrial orchids and the saprophytic *Burmannias*, though never abundant, are remarkably widespread, more so indeed than the epiphytic orchids, which, from their position in the tree tops, one would imagine to be in a much better position for wind-dispersal.

There are three terrestrial orchids in Christmas Island, one of which, *Didymoplexis pallens*, is distributed from India, through the Malay Peninsula, to the Malay Islands. It is a very short-stemmed saprophyte, almost imbedded in dead leaves in dense forest. During the fruiting period the peduncles grow to a length of twice or thrice that of the stem. The very light seeds must be borne in a rising air current to a height above the tree tops, and then carried away by breezes from Java, its nearest habitat, to Christmas Island, at least 194 miles away, where the seeds must have descended. The only orchids

in Hawaii are also three terrestrial ones of forest habitat and Polynesian affinities; their seeds must have drifted 700 miles at least, on the wind. In the same way the spores of terrestrial forest ferns, and such as grow on low tree trunks, as *Trichomanes* and *Hymenophyllum*, have drifted on the winds up through the foliage and away across the sea to Christmas Island and many other islands.

It is very common to suppose that the wind is capable of carrying light or plumed seeds or spores to vast distances, but though it is certain that the seeds of orchids and spores of ferns do travel for very great distances, and plumed seeds can travel over a hundred miles through the air, these seem to be rather exceptional cases. The actual distances to which the different classes of seeds do travel will be discussed under each heading of the forms of the organs of flight.

Wind, as it has been stated, goes in waves, and not continuously for vast distances, as may be seen by watching the waves of shadow go over wheat. Plumed seeds, dust seeds, and spores may be picked up after the wind drops, raised again, and carried along further, but winged seeds cannot be raised in this way, though in open places like deserts they can be driven along by successive blasts, so that though light spores and dust-seed can readily cross the ocean to distant islands, the distance to which plumed seed can be borne is shorter, and consequently fewer reach the remote islands, while winged seeds do not reach islands only 20 miles away. The only fruits with wings which have reached Krakatau from Java are those of *Dodonaea viscosa* and *Albizzia stipulata* and the wing-seeded *Casuarina*; but I have reason to believe that the first two are really sea-dispersed, and have evidence of the third being habitually carried about by sea. The two-winged fruit of *Gyrocarpus*, a tree which is found abundantly in Christmas Island, is mainly dispersed by sea, its wings merely serving to carry it into the water, and perhaps to act as sails to drive it along.

Over continents wind-borne seed plants may move very rapidly, especially the quick-growing annual or short-lived herbs. If we estimate that a plumed seed can fly, under good circumstances, only 25 miles distance at a flight, develop into an adult plant in a year, and the seeds fly on in the same direction continuously each year, it can spread 25,000 miles in 1,000 years—that is to say, quite round the world, or from England to China in about 370 years.

Trees—which take a long time to develop from the seed till old enough to fruit—with winged seeds or fruits move much more slowly, as I show under the account of the wing-fruited trees. The wide distribution therefore of such a genus as *Senecio*, with its very light plumed fruits, is no evidence of the great antiquity of the genus. It could easily have spread over the world in the area it now occupies in 10,000 years, and we know that it is much older than that, as it is found in the pliocene period. I mention this genus especially as much has been written to show that from its wide distribution it must be a very ancient form.

Beccari (in "Malesia," i, 215) points out that a considerable number of species are confined to mountain summits, distant from each other as much as 3,200 kilometres (2,000 miles), and that nearly related species are separated from each other by long distances. He states that from the mountain tops of the Malay Islands in November to April, at the same time of the west monsoon, the strength and constant direction of the wind are maintained for a longer time than in the low country, and it is possible that the north-west monsoon may carry small seeds from the western part of the Archipelago to the peaks of the Eastern islands, and he points out the long distances to which volcanic ashes can be carried. He urges that the light winged seeds of *Rhododendrons* could be carried, by the monsoon from the north-east, from the Moluccas to New Guinea, as well as those of *Nepenthes*, and that possibly *Leptospermum*

and *Baeckea* were brought from Australia in the opposite direction, i.e. from south-east to north-west. (He also suggests that *Leucopogon* has been brought in the same way, i.e. by winds, but the fruits of this are baccate and red and bird-dispersed.) That *Leptospermum* and *Baeckea* seeds, though not exceedingly light, may be dispersed by wind for short distances, I have little doubt, but I think that their distribution from Australia to the Malay regions by wind, in what may be called long leaps, is very doubtful. I am inclined to consider there is sufficient evidence that they are the remains of a xerophytic Australian flora which formerly spread all over this region before the invasion of the later rain-forest flora. This is, however, a question of distribution of plants, and I leave it to be dealt with under that heading.

It is, however, possible that the *Rhododendrons*, *Nepenthes*, *Gentiana*, *Primula*

The fact that plants with winged seeds and fruits, and small seed heavier than those of dust seed, are completely absent from islands a small distance away from other lands (about 25 miles), suggests that the action of wind, however strong, is not powerful enough to convey such seeds through the air to that distance, as none of these plants appear on even Cocos Island, which is constantly struck by violent typhoons.

Over continents, however, and lands occasionally connected by ice sheets, the wind plays a most important part in the dispersal of plants.

The importance of these facts on the question of distribution of plants over the surface of the globe lies in the case of a widely distributed plant whose seeds can only be " wind-borne," and are neither plumed nor dust seed, predicating a land connection at some period between the localities in which such plant is now found.

Thus the presence of the small *Gentians* with their minute seed in isolated mountains of Borneo, Java, and the Malay Peninsula, and the wing-seeded *Terminthodia* on lofty mountains in the Malay Peninsula, in Borneo and in Papua, are evidence of former land connection between these localities, with an altitude and climate similar to that of their present-day habitat. These seeds can be blown along from ridge to ridge, or to quite adjacent mountains, but it is not possible for them to be blown many miles over sea, or over land from mountain top to mountain top.

SEEDS AND FRUITS BLOWN ALONG ICE

In the Arctic regions fruits and seeds can be blown across ice to considerable distances. They can be blown on to pieces of ice which drift to a distant shore and, melting, allow the seeds to either drift or be blown on to the nearest land, or they can cross from one island to another, by being blown along the ice bridges connecting them, as readily as they can be blown along the sands of the desert. The occurrence of Arctic plants therefore in both hemispheres does not necessarily predicate a land connection between Europe and North America.

H. G. Simmons (in a " Survey of the Phytogeography of the Arctic American Archipelago ") writes : " I have seen more than once vegetable " matter heaped on sea-ice in such quantities as to protect the ice from melting, " and once at least I found accumulations of leaves and stems of different " plants, tufts of moss, fragments of lichens, etc., lying several inches thick, " and quite dry on the surface. I saw fruits of *Dryas octopetala* among the " other matter. Now, these masses of vegetable matter lay on an ice block " from the tide crack, which was already floating and might soon be carried " away. If it was stranded after a short drift, it could easily take the plant " fragments to another shore where the dry mass could be blown inland, but " in a longer drift probably all would come into the water. The sea ice is, " however, certainly of great importance for plant migration in another way. " About nine months of the year it bridges over most of the channels between " the islands, and lies dry, covered with hard blown snow, offering a smooth " surface for the wind to sweep over and carry lighter objects for any distance."

Sherard Osborne (in Journal of *H.M. Sledge John Barrow*, "Further Papers relative to Arctic Expeditions, 1855") says: "I had occasion to-day to remark " a phenomenon which often called itself to my notice, namely, the migration ' of plants. I was not botanist enough to detect the different seeds I saw ' further than merely to distinguish those of the poppy, willow, and saxifrage. ' Throughout my journey, and especially prior to the end of May, I constantly ' observed these seeds passing over the surface of the frozen floe under the

"influence of the wind. In the centre of the Polar sea these little solitary "travellers would be seen frisking on in their own odd way, now rolling "along over a smooth space, then lurking behind some hummock until a "stronger eddy wind whisked them out, and anon flying along past us some "feet above the floe." He considers that the drift of seeds by wind has been of great importance in the wanderings of plants over the Archipelago, and calls attention to the fact that the plants have their stands of fruit above the snow where, in the early spring, part of it is swept away from large areas of vegetation-covered ground. Only immediately after a heavy fall of snow practically all vegetation is covered. Very soon the wind will uncover most of the plant-covered ground, and dispersion of seeds can take place during most of the winter. He records the proportions of seeds and fruits with respect to their dispersal properties in this area as follows :—

Flying seeds or fruits, wind-borne	.. ..	42 per cent.
Light seeds ,,	.. .. ..	47 ,,
Spores ,,	.. .. ..	4 ,,
Heavy seeds, 5 species	.. ..	2 ,,
Berries or drupes	.. ..	2 ,,
Vegetative propagation	.. ..	3 ,,

The seeds he classes as heavy are those of *Astragalus* (2 species), *Lupinus arcticus*, and *Luzula parviflora* and *L. spicata*.

These might, however, be readily dispersed by wind; the pods or separate valves of the *Leguminosae* bearing seeds are easily wind-borne, and the light seeds of the *Luzulas* also would be readily carried away. Altogether he gives 189 species as wind-borne, and 15 only as otherwise distributed.

When one reflects on the immense area covered with ice during the glacial epoch, the full bearing of this method of dispersal by wind-drift across the whole north temperate zone can be appreciated. Both Lyell and Darwin noted the possibility of transport by icebergs of Arctic plants southwards in the Glacial epoch. Icebergs are known, says Darwin, to be loaded with earth and brushwood, and even the nest of a land bird has been known to be carried, and seeds might easily have been borne thus also. These icebergs have come from the breaking off of the shore ice, and no doubt the soil and heavy material came from the underlying ground from which the ice mass was detached, therefore this class of transport is rather in the nature of sea-drift; but as seeds would certainly be blown on to the ice, as shown above, they would be very probably conveyed to the more distant parts of the glaciated area.

Many of the Arctic plants found on the summits of the mountains of temperate Europe, Asia, and America, probably owed their position to the wind blowing over the ice in the Glacial period, such plants as *Dryas*, *Salix reticulata* and *herbacea*, *Betula nana*, *Papaver nudicaule*, etc.

METHODS OF DISSEMINATION BY WIND

There is a considerable variation in the methods by which wind acts as a disperser of seed. In some cases there is no special modification for dispersal, though the wind does play an important part. Such cases are the following :—

(1) **Tumble-Weeds.**—In these the whole plant or the panicle bearing fruit is detached and blown across the open country, usually scattering its seeds as it goes along. Sometimes detached bulbils or portions of the plant (usually succulents) are blown along and take root again at some distance from the parent plants. Such plants are always herbs, and often annuals. They only occur in deserts, steppes or prairies.

(2) **Light Fruits and Dust Seeds.**—These are merely blown away by the wind, and owe their dispersal to their lightness. The testa is often drawn out into thin wings which add to their lightness, as in *Orchids*, *Nepenthes*, etc. The seeds are always produced in a capsule. But there are a considerable number of plants in which a one-seeded achene is more or less winged, and is carried off by the wind. These plants are nearly always herbaceous, and in temperate regions generally lose all their leaves before the fruit is ripe, so that the panicle of fruits is fully exposed to the wind. The inflorescence is panicled or racemose, and stands up well above the ground, and the basal leaves of the plant sometimes perish away when the fruit is ripening, leaving the fruit and seeds fully exposed to the wind.

Dust Seeds (*Orchidaceae*) are extremely light, and when blown away from the capsule are able to float a long time in the air. The very minute fruits of some of the species of *Balanophora*, dust-like one-seeded nuts, are quite as light, and can be borne on the wind to very long distances, and may be included here.

Spores.—The spores of Cryptogams, Ferns, Lycopodiaceae, Mosses, Lichens, Fungi, Algae, are the lightest reproductive organs of all, and produced often in vast abundance. These float and drift on the air to great heights and distances. There is no part of the world where some are not present, and there appears to be a constant rain of the more minute kinds falling everywhere. The spores of the terrestrial Algae are the first to settle on new ground (as was shown in the Island of Krakatau after the eruption), and by their growth prepare the way for the growth of a higher vegetation. Many of the lowest spore-producing plants are so abundant that their spores swarm in the air, and the species are so widely spread that many occur all over the world wherever they can grow.

Fruits and seeds with special modifications for wind-dispersal are either winged, plumed or woolly.

Winged Fruits usually have wings formed by the bracts, sepals or petals; these are persistent and usually enlarged by continued growth (accrescent), and modified so as to cause the fruit, when detached from its pedicel, to be borne by the wind from the parent plant; or the whole pericarp of the fruit may become dry and light, and so stiff and thin that it may act as a wing. In these fruits generally, however many ovules it possesses, only one develops, so that the fruit is one-seeded. In many grasses one or more glumes or bracts persist unaltered, except for drying, and act as dispersal wings.

Winged fruits are usually to be found on trees or shrubs, especially climbers, and sometimes in tall herbaceous plants, such as *Compositae*, and in such winged fruited herbs the wing, composed of the sepals, naturally passes into a plume.

Winged Seeds are almost confined to trees and shrubs. In these the capsule splits into two or more valves and the seeds (of which a thin portion of the testa is developed into a thin wing) flutter away, usually a few at a time, and are carried away by the wind till they reach a sufficient distance from the parent. A few herbs (*Matthiola*, *Spergularia*) have slightly winged seeds, which on dehiscence of the capsule are blown to a short distance.

Winged seeds and fruits are not by any means as widely dispersed as either dust-seed or plumed seed and fruits, and—as they cannot fly far enough to cross a few miles of sea—are absent from distant islands. However, as most or all winged seeds and fruits are light enough to float, they are often further distributed by rivers, and some (*Casuarina*, *Gyrocarpus* and *Dodonaea*) are habitually distributed by sea.

Plumed Fruits possess a light, feathery portion with which they float away when detached by the wind. In some plants (*Compositae*) the flight organ is formed of the sepals, which develop into long plumed silky processes;

in others (*Geum*) the persistent style forms the plume, and in many grasses the pedicel of the spikelet is covered with silky hairs which act in the same manner. The plants which possess plumed fruits are mostly herbaceous, occasionally climbers (*Clematis*), and more rarely trees (some tree-composites, *Vernonia*, etc.). These plumed fruits frequently travel long distances and can cross the sea for 200 to 600 miles.

Plumed Seeds possess a very light tuft of silky hairs at one (rarely both) end of the seed. They are contained in a capsule which on splitting gradually releases the seeds, which then sail away on the breeze. In some cases the capsule splits gradually from the top (*Epilobium*), and in others longitudinally. The seeds are generally very numerous in the capsule. The plants are usually herbs (*Epilobium*) or climbers (*Asclepiadeae* and *Apocynaceae*), rarely trees (*Alstonia*), sometimes epiphytes (*Dischidia*, *Aeschynanthus*). They generally occur in open country like the plumed fruits, and can often fly to great distances, even across the sea for a distance of 200 miles.

Woolly Seeds and Fruits have the whole testa or pericarp covered with a mass of silky, woolly hair. The achenes of some of the Anemones are covered with wool, but woolly fruits are comparatively rare. Woolly seeds occur in the *Malvaceae* (*Gossypium*, *Bombax*) and in the *Salicineae* (*Salix*, *Populus*). The plants are usually trees, more rarely shrubs.

Woolly seeds, although they do not travel as far as plumed seeds or fruits, are capable of flying for several miles. They appear to be always absent from the distant islands.

Distances of Flight.—The distance to which seeds or fruits are blown by the wind can be measured or approximately ascertained in several ways. In the case of large winged seeds or fruit, the distances, which are comparatively short, can be actually measured, but in the case of plumed seed or of the minute dust seeds of orchids, ferns, and of small seeds like those of grasses and low herbs, this is rarely possible, as they are too small to be followed by the eye. Even comparatively large plumed seeds and fruits, such as thistle fruits and seed of *Epilobium*, can only be followed by the eye for short distances, as they frequently rise on the breeze to a considerable height and quickly get lost to view. The only way of determining the flight distance of such seeds or fruits is by noting the appearance of the plants and calculating the distance from the nearest flowering specimens. In judging this it is important to make sure that other plants could not have occurred and disappeared between the old plant and the younger one, and this is not always possible. Cases are therefore selected in which this possibility can be eliminated, such as the occurrence of the species on the mainland and on an oceanic island (i.e. an island which has never been connected with the mainland), or again when a plant is found on a high wall or roof in such a position that it must have been carried up by the wind.

In many cases seeds blown to a short distance are carried along further, after falling, by rain-wash, or by streams into which they are blown, and all these factors must be taken into consideration. Besides the actual flight from the tree to the ground, which may be but a few yards in the case of winged fruits, the fruits or seeds may continue their course by being blown along the ground by successive blasts of wind till they reach a considerable distance from the parent tree, as also frequently occurs in the case of plumed seed and fruits. Thus the furthest point to which the fruits of an Ash tree about 20 feet tall were directly blown was about 20 yards, but plants descended from this tree were found at a distance of 134 yards. In such cases it is essential that the ground must be open, either turf-fields, open downs or sand-hills.

The flight of a fruit is immediately stopped by any obstacle such as a thicket or hedge, or high rocks or walls, even in the case of small fruits by a bank, or

in open sandy deserts, etc., a mere depression in the ground, or a rock crevice where they fall out of the current of the wind. In some plants the fruits are papillose or provided with short processes, so that when they fall into cracks in brickwork or crevices in rocks, they are anchored by these processes, and again the testa of the seeds is often viscid when wetted, and when fallen into a damp crevice they adhere by the exudation of their mucilage.

In the section on Winged Fruits and Seeds (p. 71) I have given a list of such measurements of flight as I could collect. It will be noticed that the longest distance is 880 yards. This appears very short compared with the distances given for the carriage of stones and dust by hurricanes, but the short distances to which these fruits fly is confirmed by their absence from oceanic islands, even at so short a distance as 25 miles (Krakatau). If such fruits are not compelled to descend by the damp of the air over an island, it is quite intelligible that any blown out to sea by a hurricane would be more likely to fall into the sea than to alight accidentally on the island.

With dust seed and plumed fruit and seed it is different, for they are so light that they drift in the air and fall so slowly that ere they reach the water they may be raised again by wind and continue on their way; hence we find that they may travel a distance of as much as 700 miles before they come to rest.

PART II

FRUITS AND SEEDS DISPERSED BY WIND WITHOUT SPECIAL MODIFICATION

Fruits blown along by Wind—Seeds carried by Dead Leaves—Small-fruited *Compositae*—Weights of some Small Seeds, etc.—Wall Plants—Epiphytes—Flight of Achenes by Ice Filaments—Wind Dispersal of Infructescence or Whole Plants—Tumble-Weeds—Bulbils dispersed by Wind—Infructescence detached and dispersed by Wind—Dust Seed, *Orchidaceae*—Distances to which Orchid Seeds are borne—Orchids in distant Islands—Sporophytes—*Filices* (Ferns)—*Lycopodiaceae*—*Selaginellaceae*—*Equisetaceae*—*Musci* (Mosses)—*Hepaticae*—*Lichens*—*Fungi*—*Algae*.

A LARGE number of herbaceous plants which have very numerous small and light seeds in a capsule owe a great deal of their dissemination to the wind, though this is often supplemented by the action of rain after they have fallen to the ground.

Jactitation.—In most small plants the fruits are borne on long peduncles, standing well above the mass of foliage, and frequently the pedicels lengthen in fruit and stand stiffly out so as to expose the fruits more thoroughly to the wind as it sweeps over the open country, downs, meadows or mountain sides and carries the seed some distance. The springiness of the peduncle allows of its being jerked back, after the blast has passed, in such a manner that the seeds are liable to be thrown on all sides of the plant. This is well seen in such tall plants as the Foxglove (*Digitalis*), Evening Primrose (*Oenothera biennis*), and the Mulleins (*Verbascum*), where the tall racemes bend before the wind, throwing the light seed in the direction of the wind, and when the breeze drops and the raceme recovers its erect position, the seeds on the windward side are ejected in the opposite direction. As the wind constantly shifts its direction during the fruiting season of these plants, the seeds are thrown to every point of the compass. In these cases the capsules ripen gradually from the base upwards, so that the lower ones are often shedding their seeds before the uppermost flowers are even withered, and the seed-shedding may continue for a month or even more. This again adds to the dissemination, as the first fallen seeds may be blown further along or dispersed by the rain-wash of irregular showers before those in the upper part of the raceme are shed.

Eventually the whole raceme of fruits falls to the ground, and as in many plants the inflorescence is from 3 to 8 feet tall, any seeds remaining in the uppermost capsule fall at that distance from the base of the parent plant.

In many of the taller plants, especially in temperate or arctic regions, the mass of foliage produced at the base of the stem in summer dies away and disappears towards the approach of winter, or even earlier, but always as the seed ripens.

In the blue Hyacinth (*Scilla nutans*) the leaves have quite perished when the capsule is shedding its seeds. In the *Digitalis*, *Delphinium*, *Lychnis* and Hollyhocks, *Althaea rosea*, etc., the foliage, by the time the seed is being shed, is so reduced by death and decay that only a few basal leaves are left. In plants in which the one-seeded fruits or mericarps are blown away by the wind, such as the tall *Umbelliferae*, *Ferula*, *Oenanthe* and *Heracleum* and the docks (*Rumex*), the same thing occurs, and in the late autumn the dead panicles or umbels

of such plants are often to be seen still bearing the ripe fruits fully exposed to the strong autumnal gales. The death and decay of the basal foliage allow full play to the rain-wash to disperse any seeds which have fallen among the foliage, and which would be lost if the leaves did not decay and disappear. Small annual herbs and biennials which die completely after flowering and fruiting also derive much advantage from this clearing of the ground and exposure of the seeds to the action of wind and rain.

Evergreen plants, especially those which form dense masses of branchlets and leaves on the ground, have other methods of dissemination. Thus in *Linnaea borealis* the bracts of the fruits are covered with adhesive hairs for dispersal by passing deer or rabbits, to whose fur they become attached; the fruits of *Vaccinium* and *Empetrum* are baccate and dispersed by birds; *Rhododendron* has winged seeds, and *Olearia* and *Raoulia* (*Compositae*) have plumed fruits.

Capsules may contain any number of seeds from one (*Sindora*, *Myristica*) to hundreds (*Digitalis*, *Papaver*, *Verbascum*, etc.). The one-seeded capsules, however, are not wind-dispersed unless the seed is small and the capsule is winged and does not dehisce, when, correctly speaking, it becomes a samara.

In the dwarf small-podded *Cruciferae*, like *Capsella* and *Draba*, there are about 12 seeds in each of the two cells of the capsule. In *Capsella* the pod is triangular or wedge-shaped and flat. In dehiscence the outer walls of the cells become detached rather suddenly and fall off, leaving the small orange-coloured seeds attached to the partition between the cells (*replum*), from whence they are blown away by the wind. This plant is a very readily dispersed annual, and is now very widely spread in temperate regions. It is specially a weed of cultivated ground, and can grow, for a time at least, successfully in abundance only a few inches apart. The number of seed-pods on a big plant is about 234 to 264, or as much as 462, with 24 seeds in a pod, but Mr. Raffil, of Kew Gardens, states that he met with one specimen which bore 40,000 seeds. Its wide spread is not only due to its normal wind dispersal, but largely to rain-wash and adhesion to the feet of animals (the testa being mucilaginous), and by being eaten by cattle which pass and so distribute the seeds. It reached America, however, where it is now common, by human agency, being accidentally conveyed there principally in grain.

In *Draba verna* the small oval pod contains about 10 seeds in a cell. The dehiscence is much the same as that of *Capsella*—the oval thin replum on its springy pedicel blown by the wind sends the seeds away like tennis balls from a racket.

In *Cochlearia*, with 4 to 6 seeds in a cell, the whole cell-wall is thrown off with the seeds, the valve acting as a wing and carrying the seeds with it.

In the long-podded *Crucifers* (*Siliquosae*) the pod usually separates into the two valves from the base upwards, allowing the seeds to fall out one or two at a time.

The Foxglove (*Digitalis purpurea* L. (*Scrophulariaceae*)) produces an immense number of seeds. A plant in my garden, and not an exceptionally large one, bore 108 capsules, each containing about 900 minute seeds. The capsule, at first conic, splits into halves, each half dehiscing again on the inner face, but remaining so closely connected with the other half at the base that the seeds collect near the bottom and are shaken out of the cup so formed in small quantities at each puff of wind. In this plant and *Oenothera* the upper seeds in the pile at the bottom of the dehisced or partly dehisced capsule are the first to be thrown out.

The Foxglove is usually biennial, the plant only flowering and fruiting once. Of the immense amount of seed scattered from a single plant a large proportion germinate close to the spot where the perished parent plant grew,

and so a large number of seedlings are to be seen the following year crowded together, but the greater number of the seeds either fail or are washed away by rainfall. Of the overcrowded seedlings during the first year, in many cases the greater number perish, leaving only a few here and there at some distance from each other.

Occasionally the Foxglove does grow in immense abundance in certain spots for at least a year, the plants densely crowded together, and apparently successfully flower and fruit, but this does not continue. I have seen this once in Devonshire, where a portion of a hillside was of a brilliant pink from the flowers and was conspicuous from a long distance. Thomson (in " Naturalisation of Plants and Animals in New Zealand ") records the same thing, and says further :—

" It tends to die out of pasture land when not pulled out of the ground. " Whenever it is pulled out of the ground and the surface soil is thus disturbed, " fresh seedlings spring up. In one district farmers have expended as much " as £150 a year in their endeavours to clear the land of it by pulling it out ; " others who elected to leave it have been fined 50 shillings for a breach of " the Noxious Weeds Acts, and their land has become nearly clean by the " plants dying out of the pastures."

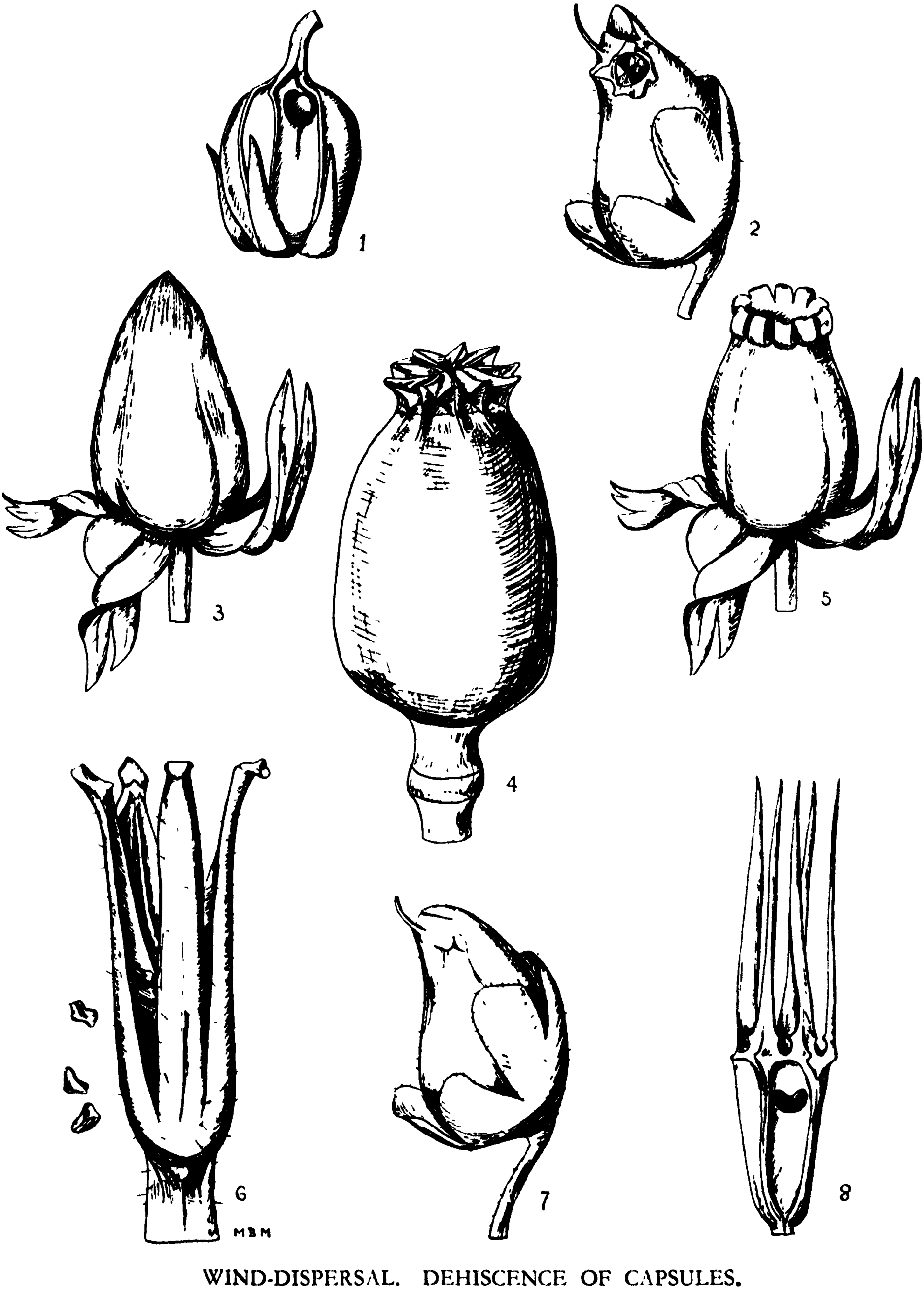
Hence it is clear that this plant to be successful requires to spread away from the parent plant, and if allowed to overcrowd, soon dies out altogether, or nearly so. One has noticed, especially after the Great War, much the same thing in the case of *Epilobium angustifolium*, where forests (especially of pine trees) were felled or burnt, this plant has come up in immense abundance. In Perth I have seen a piece of ground formerly covered by a pine wood, which had been felled, so densely covered with this plant that the pink colour of the flowers could be seen from a distance of 2 miles.

In racemose plants in which the flowers are horizontal or pendulous, and in which the fruit is capsular, it is usual for the capsule to become erect during its development and to dehisce at the apex. This is well shown in the *Liliaceae* such as *Scilla nutans*, *Galtonia*, *Lilium*, etc. The pendent position of the flower is due to the exigencies of pollination by insects.

The blue Hyacinth of our woods (*Scilla nutans*) has the flowers hanging downwards, so that the ovary points towards the ground ; after fertilisation the pedicel turns upwards, lengthens, and becomes stiff and erect ; the capsule when ripe opens widely at the top into three valves, still connate at the base and forming a cup, and the smooth round polished black seeds, becoming detached from the placentas, fall to the bottom of the cup and lie there. The leaves perish, and by this time have disappeared, so that the ground below the erect peduncle in normal cases is more or less bare. The wind blows the peduncle and so tends to shake out the seed. Every puff, as it sways to the blast and recovers itself after the puff, throws out two or three of the seeds, so that they fall on both sides of the plant, but frequently (or perhaps more commonly) some of the seeds will still remain in the cup till the peduncle falls. As the whole scape is from 12 to 18 inches tall, the seeds must fall at least a similar distance from the position of the bulb. If the ground is actually bare or open, the wind will continue to blow them along, which their round smooth form renders very easy, but usually they are carried along sooner or later by the first shower of rain. I have observed that even without this aid the seeds will fall and roll off themselves to a distance of from 3 to 6 feet from the base of the scape.

In the Evening Primrose (*Oenothera biennis* and *Oe. Lamarckiana*) the long terete capsule splits gradually from the top into four valves, and as it does so the seeds fall in a pile to the base and are gradually shaken out by the wind

PLATE I.



WIND-DISPERSAL. DEHISCENCE OF CAPSULES.

FIG. 1.—Capsule of *Campanula rapunculoides*.
,, 2.— ,, ,, *Antirrhinum majus* (open).
,, 3.— ,, ,, *Lychnis alba* (closed).
,, 4.— ,, ,, *Papaver somniferum*.
,, 5.— ,, ,, *Lychnis alba* (open).
,, 6.— ,, ,, *Oenothera Lamarckiana*.
,, 7.— ,, ,, *Antirrhinum majus* (closed).
,, 8.— ,, ,, *Campanula rapunculus*.

[*To face p.* 18.

till the last is gone. The green pod stands erect and turns brown at the tip, drying gradually downwards. A week later it commences to split far enough to let the first seeds fall out, three or four at a time when shaken. The capsule continues to split further and further till all the seeds are shed. This takes about two months (Pl. I, fig. 6). As the flowers open gradually, one or two each evening, the lower fruits commence shedding their seed before the terminal flowers are open. An average-sized plant bears 140 capsules, each containing about 180 seeds, making about 25,200 seeds on a single plant. Of these, however, a large proportion appear to be infertile. The seeds are oblong, three-angled, and smooth, and about 1 mm. long. Under ordinary circumstances a very few of these seeds come to maturity. It seems to be normally a sand-hill plant, and in open sand-hills the seed may be readily diffused by the wind blowing across the sand-hills, and also by rain-wash. It also grows by river banks, in America.

A similar method of dispersal by the slow splitting of an erect capsule from the top is common in other tall herbaceous plants such as the allied *Epilobium* (the seeds of which are plumed, and are fully dealt with under the section dealing with Plumed Seeds, p. 152), and in such species of *Iris* as have seed dispersed neither by water nor by birds, such as *I. pseudacorus* and *I. foetida* respectively. In the former instance the splitting is more rapid, and the capsule opens widely in a few days, while in the latter the capsule opens fully, the valves being very soon completely expanded, but the seeds with their bright red testa remain attached to the valves and do not fall for a long time.

In *Lilium*, *Fritillaria*, *Gladiolus*, and many such plants, the capsule becomes erect as it ripens, although the flower may be deflexed, and usually all the leaves have disappeared by the time the fruit is ripe, all that is left being the tall stalk and terminal capsule. The seeds being flat and winged are shaken out by the wind a few at a time, and fly some feet away from the plant. In all these the capsule splits slowly from the top and lets out the upper seeds first, a contrast to the explosive capsule of *Alstroemeria*, which dehisces suddenly and forcibly ejects all its seeds at once.

Enkianthus (*Ericaceae*).—This shrub is about 5 feet tall and has pendulous flowers. When the fruit is ripening the elliptic fruits turn upwards so that they are eventually pressed up against the deflexed pedicel. They dehisce part-way into 5 valves, gradually letting out the beautiful winged seeds from the top. The seeds are 1·5 mm. long, oblong and alveolate, marked like a honeycomb, with a transparent wing on each side, with processes from the hard part of the testa, giving it the appearance of a fish's fin.

In cases in which the pedicel of the capsule in pendulous flowers does not become erect before the seed is ripe, the dehiscence does not take place at the apex of the capsule, which remains pointing downwards, for if it did so, all the seed would fall out in a mass at the foot of the plant. In these cases the capsule usually opens at the base in four or five pores with short valves, the base being uppermost. This is best seen in some of the *Campanulaceae*, in many of which the flowers are pendulous and the capsules are also deflexed. In *Adenophora ornata*, *Campanula rapunculoides* (Pl. I, fig. 1), *C. rotundifolia*, *C. linifolia*, *C. Marchesettii* and *C. trichocalycina*, the capsule is subglobose, or urn-shaped and decurved. It opens at the base by from three to five pores, the mouths of which are surrounded by valves. In wet weather these valves swell up and close the pores again, but in dry weather they are open and release the seeds. In *C. rotundifolia* and its allies the dehiscence continues as the seeds fall, so that only the ribs of the capsule remain, eventually allowing the seeds to escape also at the sides. In *Campanula rapunculus* the capsule becomes erect in reopening, and is wineglass-shaped, narrowed at the bottom

and dilated upwards. In this the pores open at the top of the capsule in dry weather, closing up during rains (Pl. I, fig. 8).

The Campions (*Silene* and *Lychnis*) have erect bottle-shaped capsules, which open at the top in dry weather by the reflexing of a number of small teeth. In rainy weather they close over again and shut the mouth of the fruit. The seeds are very numerous and small, usually reniform (Pl. I, figs. 3 and 5). A single plant of a white Campion (*Lychnis alba*) was in a bed in my garden, and for some years did not spread. It was visited by the moth *Dianthecia cucubali*, and very soon spread rapidly. Many of the plants which were derived from it had pink flowers, some had pure white, and some white tinted with pink. I conclude, therefore, that the moth had fertilised the white-flowered *L. alba* with pollen of the pink *L. diurna*, and that these coloured forms were hybrids. The seeds spread (doubtless by the wind), not only to the next bed, but across a grass plot to a distance of 25 yards. They would probably have gone further, but were stopped at that point by the house.

In the Snapdragons (*Antirrhinum majus* and *A. orontium*) the capsules are erect, flask-shaped, and open at the top by four pores, the valves of which close in wet weather and open in dry weather. The seed is gradually shaken out by puffs of wind swaying the raceme about, but though—owing to the small size of the pores—only a few seeds are shaken out at a time, the capsule becomes quite empty in a few days (Pl. I, figs. 2 and 7).

The Poppies (*Papaver*, *Meconopsis*, etc.) have a similar method of dispersal to that of *Antirrhinum*, but the capsule is urn-shaped and borne erect singly on a slender pedicel. The pores are numerous and placed at the top of the capsule beneath the sheltering edge of the large persistent, orbicular stigma, which extends all round over the pores and prevents, as by an umbrella, the entrance of rain. The valves of the pores also swell up in wet weather and make the wetting of the seeds impossible (Pl. I, fig. 4, *Papaver somniferum*).

Linaria vulgaris has a capsule similar to that of *Antirrhinum*, which opens by pores at the top with valves in dry weather, and which close again in rain. Its seeds, emitted gradually by the shaking of the raceme, are winged with a circular wing and are blown by the wind to some distance.

In follicles like those of *Delphinium*, of which four or five stand together erect on the branches of the raceme and open at the top, this system of closing the opening is not required, since the follicles also open along the inner edges and slightly separate, so that rain-wash does not collect in the follicles. Nor is it necessary in capsules which slowly split downwards, like *Oenothera*, for here any rain that falls on the opened portion would escape between the separated valves, and, in any case, could only wet the uppermost seed, which the further dehiscence of the capsule would quickly set free.

The object of protecting the seeds by these methods from the entrance of rain into the globose or urn-shaped capsules is not in any way to prevent the germination of seed therein by their being wetted, but solely to facilitate their escape, a few at a time, in dry weather. If water is let into a Poppy head or Snapdragon capsule, the seeds adhere together in a mass and cannot be shaken out. Even a small drop of water entering the capsule through a pore will cause the uppermost seeds to stick together and form a block to the exit of the lower ones, even if these remain dry. The seeds individually are not injured by wet, for they are frequently carried away by rain-wash after they are discharged from the capsule.

In all these cases the action of the wind is required to throw out the seeds of the early-fruiting *Silenes*, *Lychnis*, *Antirrhinum* and Poppies, by the light summer breezes, while the later-fruiting *Oenotheras*, *Verbascums*, and many others gain an advantage from the more violent windstorms of September and October.

a

Some of these minute seeds must be actually lighter than the grains of sand blown to the Canaries and Naples from the African coast, and a few of the above-mentioned plants do occur in the Canaries, e.g., *Arenaria serpyllifolia*, but they are all plants likely to be introduced by man, and we have no evidence of such plants crossing the sea by air.

A. T. Urquhart (Trans. New Zealand Institute, xiv, 364) writes of *Epacris microphylla*, an Australian plant occurring also in New Zealand, that its seeds are dispersed by wind, and that he cannot account for its appearing in New Zealand, on the south side of Manakau Harbour, otherwise than by suggesting that the seeds were carried by wind 1,300 miles from Australia.

E. purpurascens seems to have got to nearly the same spot in the same way. I think it is impossible for these plants to have been introduced by wind. As they are apparently both sea-sand plants, it seems more likely that the seeds were either sea-drifted or brought accidentally in ships, perhaps in ballast.

In oceanic islands such small-seeded plants are strikingly absent, and when they do appear they are always associated with human invasion.

The spread of Beech nuts (*Fagus sylvatica*) by wind is treated of by Mr. A. S. Watt (*Journ. Oecology*, xiii, p. 30) in the " Ecology of British Beech Woods."

The distance to which the seeds of the herbaceous plants fly in ordinary cases in a fairly light breeze are naturally short. Miss M. F. Boynton gives some instances (in her "Observations on the Dissemination of Seeds," *Bot. Gazette*, 1895, 502). An *Oenothera biennis*, 35 and 40 inches tall, shed 12 seeds at a distance of between 35 and 40 inches from the plant, and 60 seeds between 23 and 63 inches. In another plant 30 inches tall, with the lowest pod at 11 inches from the ground, the nearest seeds fell 22½ inches away, but the fallen seeds were most numerous at a distance of 13 feet. A *Datura Stramonium*, 44 inches tall, with the lowest pods 27 inches from the ground, threw some seeds as far as 10 feet from the plant, but the majority fell 6 feet away. The distances of fall in proportion to height will be seen in this series to be very varied; probably the difference between the two *Oenotheras* was due to variation in the breeze at the time. It is quite clear that in plants no better provided with dispersal apparatus than these are, the seeds do fly to some distance from the mother-plant, sufficiently far for the furthest ones to develop unaffected by the proximity of the parent. The progress of these herbs throughout the world is apparently more rapid than would be suggested by figures such as these, but in all cases we must reckon with the additional wider and more rapid diffusion by rain-wash which follows the fall of the seeds. At least the seeds fall clear of the mother-plant, and are scattered away from each other, and that is about as much as can be expected from this simple dissemination method.

Fruits Blown Along by Wind.

Kerner mentions the rolling of the fruit of *Blumenbachia Hieronymi* (*Loasaceae*), a South American plant, by wind across the plains. The fruit is very light; though 2·5 cm. (an inch) through, it only weighs 0·34 grain when dry. As soon as the seeds are ripe the fruit stalk withers, and the round fruit left lying loose on the ground are rolled away by the gentlest breeze. If they are stopped anywhere and get wetted with rain, the openings which are already formed in them become enlarged, and a quantity of wrinkled seeds drop out.

The capsules of *Mesembryanthemum* in South African plains behave in the same way. They are closed in dry weather and open in wet. When moistened the valves covering the ventral sutures of the loculi open back, dehiscence takes place along the sutures, and the seeds are washed out. While closed in the dry period they are blown along the sandy deserts.

The fruit heads of *Brunsvigia multiflora* (*Amaryllidaceae*) are said by Phillips to be 2 feet across, and are blown across the veldt of Africa, scattering the seeds as they go.

Seeds Carried by Dead Leaves.

It so happens that (apparently not infrequently in the autumn) seeds fall among dead leaves and may adhere by viscidity or be caught in the curl of the withered leaves, and be blown and thus carried by the wind to a great distance. The distances to which leaves may be carried by wind in open places has been already recorded. Seeds and small fruits viscid when wetted might readily be dispersed by this means.

Mr. K. W. Braid tells me that on one occasion he found dead and curled leaves of the Beech tree (*Fagus sylvatica*) drifted to a considerable distance on the downs in open country, which bore with them minute snails and the seeds of *Oxalis acetosella* which are very sticky.

Sturm, in his account of *Adoxa moschatellina*, says that the wind blew leaves to him which bore three seeds of the *Adoxa*. This little herb has a cluster of viscid fruits, like white currants, on a peduncle, which, when the fruit is ripe, bends down towards the ground, and may be spirally twisted in the centre, at which point the peduncle is apt to break off. In any case this woodland plant is likely to place its viscid fruit on a fallen leaf, to which it might adhere and so be blown away to some distance.

T. G. Lemmon (in *Bot. Gaz.*, ii, 146) describes the dispersal of the seeds of *Leucocrinum montanum* (*Liliaceae*), a dwarf plant of California, in in which the capsule is almost buried beneath the ground in the tuft of linear narrow leaves, which are 4 to 6 inches long and about $\frac{1}{4}$ inch wide. He was puzzled to account for the complete disappearance of the seeds after dehiscence till he found that they fell into the sheathing portion of the leaves and were blown away, enclosed in them, during the winter.

Another odd way of dispersal of a similar nature is described by T. Meehan (*Bot. Gaz.*, iv, 207). He observed a number of small seeds attached to a bunch of the viscid dried stems of *Cerastium nutans* in North America. This kind of accidental dispersion by the blowing away of the withered stems may not be common or normal, but it is clear that in dry localities where viscid herbs are abundant this might happen from time to time and be effective in the dispersal of minute seeds.

Small-Fruited Compositae.

Many of the *Compositae* have their small one-seeded fruits (achenes) plumed or armed with acute sepals, so that they can be dispersed by attachment to animals, but in a large number the achenes are unprovided with additional apparatus for flight or for any other means of dispersal. For dissemination they depend only on the lightness of the said fruit, which is usually flattened and thin. By this means only they are borne by the wind to a distance from the parent plant. It is true that most, if not all, of these light achenes float on water, but most of them are not adapted for growth in wet places, at any rate among the British species, and thus this means of dispersal is not available to any extent. The achenes of the Tansy (*Tanacetum vulgare*), a river-bank plant, however, do float, and are clearly frequently dispersed by water, as also is the case of *Bidens tripartita* and *cernua*, both of which, however, are very largely dispersed by adhesion to animals.

But in this section I deal with *Compositae* which possess none of these advantages, and are simply disseminated over land by the winds blowing their light achenes along. They are usually tall plants, but if dwarf, the flower head is raised well above the foliage ground with full exposure to the wind.

Rudbeckia laciniata, a native of North America, is a herb over 6 feet high. The very numerous achenes are borne on a conical receptacle $1\frac{1}{2}$ inches (4 cm.) tall. When these are ripe the outer ray-florets of the head are withered and gone, leaving only the cone of achenes on its peduncle fully exposed to every puff of wind. The achenes are oblong and four-angled, $\frac{3}{16}$ inch long and $\frac{1}{16}$ inch wide. They are very light. They become detached and are blown away a few at a time only, most of them falling a few yards distance from the plant, though I have found in my garden young plants, the achenes of which must have been blown across a grass plot 15 yards from the mother-plant. In open country, with stronger winds, they no doubt travel much further.

Chrysanthemum leucanthemum, the Ox-eye Daisy, has flat oblong achenes in a flat or nearly flat head, the ray-florets disappearing when the fruit is ripe.

They fly in the wind to some distance, and I have found plants derived from achenes of a plant 8 yards away.

Chrysanthemum parthenium is a low-growing bushy plant, usually about 8 to 12 inches tall, with numerous flower heads, bearing generally about 20 ripe achenes in each. In many of these *Compositae* a number of the tubular florets are unfertilised or, at least, never develop into fruit. The ray-florets disappear on the ripening of the fruits, and the very light achenes, $\frac{1}{16}$ inch (2 mm.) long, are blown away. These achenes are light enough to float in water. I have no record as to the distance they can fly, but seedlings appear in all parts of my garden, and they clearly travel farther and more easily than *Rudbeckia* and the Ox-eye Daisy.

Achillea millefolium (the Yarrow).—This plant seems to spread rapidly. It owes a good deal of its wide distribution to human agency, being carried about in turf, and is very adaptive, and able to stand droughts better than most of our herbs. In the great drought of 1921, when the grass was completely dried up, the only green plant on my lawn was the Yarrow. The heads of flowers stand up well above the ground, and in the fruiting season consist of a number of papery bracts, the remains of the flowers, and a comparatively small number of very light, flat achenes, 3 mm. long and 1 mm. wide. During the early windy winter season the whole head is blown away in pieces. The achenes are quite flat, with both edges elevated into a thickened ridge, forming a kind of wing. The plant is abundant on the abandoned railway track near Turnham Green, a spot where almost all the vegetation springing up consists of plants with wind-dispersed seeds or fruits. Thus the following are the plants I see growing there :—*Tussilago farfara*, *Epilobium angustifolium* and *Erigeron canadense* (plumed fruits and seeds), *Linaria vulgaris* (winged seeds), *Acer pseudoplatanus*, *Betula alba* (winged fruits), *Arrhenatherum avenaceum* (grain enclosed in glumes), *Artemisia vulgaris*, *Matricaria inodora*, *Achillea millefolium*. In some of these *Compositae* the achenes, when ripe, become detached and fall from their erect position so as to lie loose in the cup formed by the involucre, the bracts which form it as they dry becoming inflexed over the fruits. By this means the achenes are prevented from being all blown away together, but as the receptacle is shaken by the wind a few at a time are thrown out. Good examples of this are to be found in the Daisy (*Bellis perennis*) and *Matricaria discoidea*. The involucre is horizontal in flower, and when the ray-florets on the Daisy are fallen away, the achenes ripen on the tall conic receptacle and fall to the base. The involucre, now withering and drying, closes over the loose achenes. The migration of the achenes is continued frequently by rain-wash. In *Matricaria discoidea* much the same thing happens, but the receptacle is flat and not conical, and the achenes are partly dispersed, when blown away, by rain-wash, but to a much greater extent by adhesion to the feet of animals and human beings. The distance that they are carried by wind in a moderate breeze I found, when held at about 2 feet from the ground, was only about 3 or 4 yards, but this is certainly far enough to start them on their further travels.

In the Nipplewort (*Lapsana communis*) the seeds are comparatively heavy. The involucre is tubular and never expands, but becomes dry, when the achenes are thrown out 1 or 2 at a time by the wind. There are about 12 in a head. This plant seems to move very slowly, as plants in my garden have hardly spread a couple of yards in a dozen years. It grows usually in clumps together, showing how slow its dissemination is, but I have found plants on walls at Exeter 5 feet from the ground, where they must have been blown upwards. It chiefly occurs in Britain in cultivated ground, and owes much of its distribution to human agency, and has probably been introduced in this way to the Canaries and Madeira Islands.

WEIGHTS OF SOME SMALL SEEDS, ETC., IN GRAINS.

In this list of small seeds I have taken the figures from various authors, viz., F. Nowers ("Dispersal of Species," Burton-on-Trent Nat. Hist. Soc., 1906, 144), marked (N); Kerner (Nat. Hist. Plants, ii, 851), (K); Troup ("Sylviculture"), (T); Wallace ("Darwinism"), (W); Beccari ("Malesia"), (B); Rolfe (*Orchid Rev.*), (R), and I have (with the assistance of Mr. S. Hunt) reduced them to decimals of a grain from the various classes of weights given.

	Grains.	
Weight of Quartz :—		
Grains found 600 miles from land ..	·00005	(W)
" " 700 " " "	·00004	(W)
Weight of Seeds :—		
Goodyera repens	·000086	(K)
Stanhopea oculata	·0000463	(K)
Dendrobium attenuatum	·00008719	(B)
Cycnoches chlorochilum	·000055555	(R)
Monotropa hypopitys	·0000463	(K)
Sagina procumbens	·0000833	(W)
Pyrola uniflora	·0000617	(K)
Aeschynanthus sp.	·0003086	(B)
Sempervivum acuminatum	·0003086	(K)
Rhododendron verticillatum	·0004321	(B)
Nepenthes phyllamphora	·0005401	(B)
Gymnadenia conopsea	·000123456	(K)
Dendrobium attenuatum	·0004321	(B)
Parnassia palustris	·000463	(K)
Umbilicus erectus	·000926	(K)
Orobanche ionantha	·0001543	(K)
" *minor*	·0008	(N)
Sedum maximum	·000617	(K)
Orchis maculata	·00015	(W)
Penthorum sedoides	·00125	(W)
Adina cordifolia	·001458	(T)
Hymenodictyon excelsum	·009115	(T)
Lepigonum (*Spergularia*) *marginatum*	·00108	(K)
Spiraea aruncus	·001234	(K)
Veronica aphylla	·001543	(K)
Capsella bursa-pastoris	·002315	(K)
Euphorbia peplus	·006327	(K)
Trifolium repens	·009105	(K)
Astilbe rivularis	·00203	(W)
Papaver dubium	·0208	(N)
" *rheas*	·02135	(N)
Cedrela toona	·05469 to ·03646	(T)
Eucalyptus globulus	·0673 to ·04654	(T)
Casuarina equisetifolia	·021875	(T)
Hypericum perforatum	·0191	(W)
" *hirsutum*	·01402	(W)
Draba verna	·0555	(W)
Mimulus luteus	·0343	(W)
Antirrhinum majus	·0221	(N)
Saxifraga coriophylla	·0133	(W)
Oenothera rosea	·0156	(W)

As Wallace points out ("Darwinism," p. 365), many of the seeds which are heavier than the quartz grains are irregular in outline, and some compressed, and consequently would offer a larger surface to the air, and also that their rough surfaces and dilated parts of the testa would increase the friction and render the uniform falling through still air considerably less than in the case of the smooth solid quartz grains.

"With these advantages it is a moderate estimate that seeds ten times the "weight of the quartz grains might be carried through the air by a violent "gale and under the most favourable conditions.

"It appears, therefore, to be absolutely certain that every autumnal gale "capable of conveying solid mineral particles must also carry numbers of small "seeds at least as far, and if this is so, the wind alone will form one of the "most effective agents in the dispersal of plants."

It seems to be very probable that a vast number of small-seeded plants (such as *Sagina* and *Pyrola*, *Parnassia*, etc.), even without special flight organs, are carried rapidly across continents, whether mountainous or steppe land. The absence, however, of these small-seeded plants from remote islands suggests that the favourable conditions for their flight must be scarce.

The seeds of *Eucalyptus* are very light, and being borne on trees of considerable height can be carried by the wind to very great distances. E. P. Turner (in "The Vegetation of Tarawera Mountain, New Zealand," Trans. New Zealand Inst., lix) found a tree of *Eucalyptus globulus*, the Blue Gum tree, growing on the volcanic deposits, the nearest other tree to which whence the seed could have come was 5½ miles away.

Wall Plants.

Many rock or wall plants climb to considerable heights up cliffs or walls by their seeds being blown violently against the face of such obstacles, and the wind, rising over such obstacle, carries the seeds up to some crevice therein in which they lodge. Here it is essential that the seeds should be tolerably light or provided with plumes or wings. A wall-top flora usually consists in England of a number of plants with small or light seeds or one-seeded fruits, a few with plumed seeds, *Taraxacum*, *Epilobium*, *Centranthus* and *Senecio*, and a few bird-dispersed ones, *Solanum dulcamara* and *Taxus baccata*, and some transported by ants.

As most of the last three groups are more adapted for growth in a sufficiently deep soil and less so for the limited amount of soil in a wall, they are naturally scarcer.

The furnishing of a wall with vegetation is usually effected in this way. First a certain amount of dust and dry soil is blown up so as to rest in the crevices, then the blue-green terrestrial *Algae* settle on this soil and adapt it for the growth of mosses. As these decay the soil increases in amount and becomes suitable for the spores of ferns, which are the next plants to appear, should there be any in the neighbourhood; these are followed by flowering plants with small seed which can be blown up the wall and lodge in the crevices.

Thatched roofs and bared cliffs and such places are furnished in the same way. I treat of this migration of plants here as it is mostly due to wind-action, and it throws some light on the dispersal of small light seeds by wind.

It must be noted, however, that plants which can grow in such situations can make their way up to considerable heights gradually by merely dropping the seeds or small fruits into crevices from the highest point of the inflorescence, and these, developing into plants, continue the upward course.

Parietaria officinalis seems to climb up walls and towers very largely in this way. In Christmas Island I found *Crinum asiaticum* growing on the upper part of a cliff over the sea. The large seeds of this plant were doubtless drifted to the island by sea, and grew originally at the face of the cliff, which was of coral-reef and contained many hollows in which the plant could grow. The peduncle bearing the fruit is about 3 feet tall, and when the seeds are ripe they drop, by reason of the fall of the peduncle, into a hollow 3 feet above the parent plant, and one or more germinate and grow, and so on upwards. When I found the plant, the peduncle had recently fallen and the seeds lay in a hollow about 3 feet above the parent plant. In examining the vegetation of walls and cliffs this system must be taken into account, but where this is not possible the vegetation on the wall-tops may safely be considered to have reached its position by direct wind-action, and will illustrate how great a part is played by the wind in diffusing small seeds and fruits which possess no special modification for the purpose. I give some illustrative examples.

Cotyledon umbilicus.—I observed in Guernsey this plant growing on pinnacles of rock 10 to 12 feet high, in such positions impossible for it to have reached in any other way than by the direct action of wind, the faces of the pinnacles being quite smooth and without any crevices. The seeds are very small and light. (*See also under* Epiphytes, p. 30.)

Orobanche hederae.—This is parasitic on ivy, and the plant is usually found at the base of a wall on which ivy is growing. I have found it, however, in Guernsey growing on an ivy-covered wall 4 feet from the ground, and Marquand (in the "Flora of Guernsey," p. 136) records it at a height of about 8 feet from the ground on the north wall of St. Martin's churchyard.

Linaria minor (*Scrophulariaceae*).—A small plant of this was found growing in a crack of the stonework of the obelisk on Ballard Down, Swanage, about 1 foot from the ground. I could not find another plant of it in the neighbourhood, and it was probably blown from some considerable distance.

On the top of the Agglestone rock in Studland Heath, about 5 feet from the ground, were plants of *Rumex acetosella*, *Erica cinerea* and *Deschampsia caespitosa*. The seeds of the heath are very minute, but the whole capsule, when ripe, is enclosed in the marcescent corolla, which is detached from the raceme and blown away, scattering the seeds as it goes. The grains of *Aira* are included in their glumes when dispersed, the glumes acting as wings. These seeds must have been blown up to the top of the rock from the heath below.

Malva sylvestris occurs frequently on walls and towers at great heights. I have seen it on Corfe Castle on one of the towers at about 80 feet high, and on the ruined tower of South Walsham Church in Norfolk, at about the same height from the ground. Higher up on the same tower was abundance of *Hordeum murinum*. The seeds of the Snapdragon (*Antirrhinum majus*) are constantly carried by wind up the sides of ruined walls, and *Dianthus caryophyllus* has in like manner ascended the walls of Rochester Castle.

Besides these, I have seen or found recorded the following plants on the tops of walls or roofs at a considerable height from the ground where only wind could carry them :—

Ranunculus acris	At a height of 7 feet.
Papaver argemone	At a height of 8 feet.
Cardamine hirsuta	A few feet.
Capsella bursa-pastoris ..	A few feet.
Cochlearia officinalis	On walls and rocks.
Sisymbrum officinale	A few feet.
Draba aizoides	A few feet.
Lepidium campestre	A few feet.

Arenaria serpyllifolia	6 feet.
Cerastium triviale	7 feet.
" *viscosum*	7 feet.
Stellaria media	Thatched roofs, 7 feet.
Dianthus plumarius	Walls.
" *caryophyllus*	Walls.
" *caesius*	On the Cheddar Cliffs.
Holosteum umbellatum	Walls.
Sagina apetala	12 feet.
Hypericum hirsutum	20 feet. Fountains Abbey.
Corydalis lutea	Up to 15 feet. Possibly seeds carried by ants.
Viola odorata	Up to 6 feet. Possibly carried by ants.
Geranium Robertianum	Up to 6 feet or more.
Trifolium minus	3 or 4 feet.
Anthyllis vulneraria	3 or 4 feet.
Medicago lupulina	Possibly bird-carried.
Saxifraga tridactylites	Up to 12 feet. Exmouth.
Sedum acre	Common on roofs.
" *reflexum*	Common on roofs.
Pimpinella saxifraga	20 feet or more. Fountains Abbey.
Foeniculum vulgare	12 feet or more. Lime kiln, Slapton, South Devon.
Crithmum maritimum	On cliffs.
Galium aparine	7 feet. But much transported by birds.
Bellis perennis	A few feet.
Lapsana communis	6 feet.
Centaurea nigra	30 feet and more. Fountains Abbey.
Scabiosa columbaria	12 feet. Fountains Abbey.
Campanula rotundifolia	20 feet and more. Fountains Abbey.
Samolus valerandi	High upon cliffs.
Veronica agrestis	8 feet.
Digitalis purpurea	6 to 8 feet.
Scrophularia nodosa	10 to 12 feet.
Verbascum thapsus	10 to 12 feet.
Thymus serpyllum	A few feet. Bude.
Lamium purpureum	5 to 12 feet. Perhaps ant-carried.
" *album*	6 feet. Perhaps ant-carried.
Origanum vulgare	12 feet and more. Fountains Abbey.
Plantago lanceolata	12 feet and more.
" *coronopus*	2 feet.
" *major*	12 feet. Kirkstall Abbey.
Urtica dioica	8 feet. Sonning, on walls.
Poa annua	About 12 feet. Common.
Lolium perenne	About 12 feet.
Dactylis glomerata	About 12 feet.
Festuca myurus	About 12 feet.
" *ovina*	12 feet. Fountains Abbey.
Bromus sterilis	On roofs.
Hordeum murinum	80 feet. On walls.

Many other plants might be added to the list of wall plants whose small seeds were borne to some height from the ground by wind. I have not included in the above list the even more numerous plants with plumed fruit, such as

Epilobium, *Sonchus oleraceus*, *Senecio squalidus*, *S. vulgaris*, *Prenanthes muralis*, *Crepis virens*, *Hieracium*, *Centranthus*, etc., nor the plants with baccate or drupaceous fruits, the seeds of which are dispersed by birds, such as *Ribes grossularia*, *Solanum dulcamara*, *Taxus*, *Ficus*, etc., as the value of the list given above lies in showing that seeds and fruits of plants, often dwarf, which have no other means of dispersal than their lightness (except the more restricted action of rain-wash), from their wide area of distribution, and in some cases abundance, must move fast and far. Judging by the absence of these small-seeded plants from oceanic islands, the distance to which they can be blown through the air seems comparatively short. The observations, however, were taken in the lowlands of England, and it is probable that the violent wind storms of the steppes and mountain districts may carry these small seeds further, and hence faster, across such areas.

Though the seeds of such dwarf plants as *Thymus* are readily blown across open flat country, plants with longer peduncles or stems can undoubtedly be moved faster; *Plantago lanceolata* is not only to be found higher up on walls, etc., than *P. coronopus*, which I have only found on walls 1 or 2 feet from the ground, but it is the first plant to appear in abundance on ground which has been cleared of turf on the downs. Its long, weak peduncle assists very much in throwing the seeds into the air to be borne along in the wind.

O. F. Richard (in " Florule des Cloches et toitures des Eglises de Poitiers," Vienne), gives an extensive list of the plants he found growing on the walls and towers of churches in Poitiers.

He gives no actual heights at which the plants were growing, but says they were found only at the highest parts of the walls above the buttresses and porches. He points out that some of them may have been carried up to the towers on twigs carried by crows in building their nests, and he might have added sparrows (*see under* Birds' Nests, p. 512), and some on the clothes and shoes of workmen and visitors; some undoubtedly were swallowed and passed by birds. I have arranged them according to obvious methods of transport. Wind-dispersed: *Acer pseudoplatanus*, *Centranthus ruber*, *Erigeron canadense*, *E. acre*, *Inula conyza*, *Senecio vulgaris*, *S. Jacobaea* (rare), *Cirsium lanceolatum* (rare), *Carduus nutans* (rare), *Hypochaeris radicata*, *Thrincia hirta*, *Taraxacum dens-leonis*, *Chondrilla juncea*, *Sonchus oleraceus*, *S. asper*, *Barkhausia taraxacifolia*, *Crepis virens*, *Hieracium naevuliferum* (plumed fruits), *Ulmus campestris*; *Poa annua*, *P. nemoralis*, *P. pratensis*, *P. compressa*, *Dactylis glomerata*, *Festuca rigida*, *F. duriuscula*, *Bromus sterilis*, all wind-dispersed grasses, but possibly also brought by birds for nests. By birds swallowing and passing seeds: *Ribes grossularia*, *Prunus cerasus*, *Rubus fruticosus*, and perhaps *Chenopodium album*, *Medicago lupulina* and *Atriplex angustifolia*. The rest are small-seeded plants of which the seeds might be blown up on the walls—*Cheiranthus cheiri*, *Sisymbrium thalianum* (rare), *Capsella Bursa-pastoris*, *Reseda lutea*, *Arenaria tenuifolia*, *A. serpyllifolia*, *A. leptoclada*, *Hypericum perforatum*, *Geranium molle*, *G. rotundifolium*, *Erodium cicutarium*, *Medicago sativa*, *Lotus corniculatus* (rare), *Poterium sanguisorba*, *Sedum album*, *S. acre*, *Saxifraga tridactylites* (rare), *Petroselinum segetum*, *Galium mollugo*, *G. anglicum*, *Campanula rapunculus* (rare, very rare in the district), *Wahlenbergia erinus*, *Echium vulgare* (adhesive), *Veronica agrestis*, *Origanum vulgare*, *Calamintha acinos*, *Ballota foetida*, *Plantago lanceolata*, *Polygonum aviculare*, *Mercurialis annua*, *Parietaria officinalis*.

Massart (in " l'Intervention des Animaux dans l'evolution des Vegetaux," 1893, p. 20), writes that the farm buildings in Norway are often covered with turfs of grass on which a special vegetation is not slow to appear, and among the trees and shrubs he found there were *Pyrus aucuparia*, *Empetrum nigrum*, *Vaccinium uliginosum*, *V. myrtillus* and *V. vitis-idaea*, and I can add *Fragaria vesca*, which I have seen on roofs abundantly at Bergen, Norway. He does

not mention the wind-dispersed plants, which are abundant also, as he is only dealing with bird-dispersed plants.

EPIPHYTES.

In the tropics the greater part of the epiphytic plants on the trunks and boughs of the forest trees are wind-borne. Ferns, mosses, hepatics, lichens, orchids, plume-seeded *Bromeliaceae*, *Aeschynanthus* (*Gesneraceae*), *Asclepiadaceae*, *Hoya* and *Dischidia* and *Rhododendron* with their fine-winged or plumed seed, form frequently small gardens covering the boughs at a great height from the ground. They are accompanied also by a number of plants with baccate or drupaceous fruits, such as *Medinilla*, *Pachycentria*, *Ficus*, some *Vacciniaceae*, *Araceae*, *Fagraea*, *Hydnophytum*, of which the seeds are disseminated by birds who rest on the branches. The greater number, however, are wind-dispersed plants. The main essential for an epiphytic flora of this nature is continuous moisture and warmth. They are absent from cold and hot dry climates almost entirely. In temperate climates we have few real epiphytes except cellular cryptogams, but in pollarded willows and some other trees we find a considerable flora of plants commonly growing on the ground, but which have established themselves in the soil accumulated in the tops of these trees. Exclusive of the mosses and lichens which grow on branches of trees in English woods, the chief true epiphyte found here is *Polypodium vulgare*, which is often to be seen on the branches of oaks and other trees. In Devonshire I found *Cotyledon umbilicus* growing epiphytically in Courtenay Walk, Bolthead, on branches of oak trees, and one on a chestnut, at heights of from 2 or 3 to 40 feet above the ground. The very light seeds were undoubtedly transported there by the wind from numerous plants growing on the ground. Mr. Edgar Thurston reported to me a number of cases of cultivated Rhododendrons growing as epiphytes on the trunks and boughs of the oaks *Quercus robur* and *Q. suber* in Cornwall in several localities, and from Mrs. Rogers, of Mawnan, Falmouth, I received an account of the occurrence of *Griselinia littoralis*, a New Zealand shrub, growing epiphytically on *Pinus insignis*. The fruits of this plant are one-seeded, black, and a quarter of the size of an ivy berry. They were evidently transported to the pines by birds, probably thrushes. Mrs. Rogers says the plant is very prolific and scatters its seeds everywhere. The epiphytic ones are in three forks of the pine, the lowest about 11 feet from the ground, the others about 5 or 10 feet higher up. The plants are about 28 inches in diameter and 2 feet tall, and have been there for years. They also appeared in the top of a Chinese palm (probably *Trachycarpus*). *Griselinia* does not appear to be epiphytic in New Zealand.

Of the plants growing in the tops of willows various authors have written. It will be noticed that the seeds in these cases are by no means always wind-dispersed. In some cases the seeds are blown up into the tops of the pollards, but in addition there are a number of plants with drupes or berries of which the seeds have been evacuated by birds, and in other cases the seeds, or living fragments capable of growth, of the plant have been brought by birds to form nests. Occasionally, too, one finds a few commonly transported by ants which may have made nests in the trees. One may compare the pollard-willow flora with the wall and roof flora. Many will be found identical, but, as a rule, birds contribute very little to the flora of roof and wall, and many bird-dispersed plants cannot grow on the small supply of soil in these places, though they can do so in the top of the willow. I here give an account of the pollard flora as described by various writers :—

M. C. Thomas (*De Geogr. Bot.*, 13, p. 358) gives an account of some in a paper entitled "Vegetation epiphyte sur Saules têtards." He examined the

flora of eight Pollard Willows in St. Dizier, Haute Marne, France, and found the following plants, to which list I have added the probable way in which the plants arrived in these spots. They are arranged in order of abundance :—

Galium aparine (fruits adhesive, possibly in bird-nests), *Epilobium montanum* (seeds plumed, wind-borne), *Rubus idaeus* (drupelets, bird-borne), *Galeopsis tetrahit* (disseminated by ants), *Nepeta glechoma* (disseminated by ants), *Geranium Robertianum* (probably wind-borne or by explosion), *Lonicera xylosteum* (bird-borne), *Geum urbanum* (fruit adhesive), *Poa* sp. (wind-borne), *Sambucus nigra* (bird-borne), *Solanum dulcamara* (bird-borne), *Urtica dioica* (adhesive), *Cerasus avium* (bird-borne), *Fraxinus excelsior* (wind-borne), *Lamium album* (wind-borne or by ants), *Ulmus campestris* (wind-borne), *Dactylis glomerata* (wind-borne), *Chelidonium* (ant-dispersed), *Fragaria vesca*, *Pyrus aucuparia*, *Ribes rubrum* (bird-borne), *Anthriscus sylvestris* and *Heracleum sphondylium* (wind-borne), *Taraxacum dens-leonis* (wind-borne), *Calystegia sepium* (possibly the plant climbed up the tree), *Humulus lupulus* (wind-borne).

The largest number of these species are wind-borne. *Galium aparine*, the commonest, though adhesive, is more likely to have been carried by a bird to form a nest, as it has been recorded as having been used for this purpose. It is very possible that many of the drupes and berries were brought by birds to their nests in order to feed their young, and the seeds regurgitated by birds, such would be *Cerasus*, *Rubus*, *Sambucus*, etc. This subject, however, is referred to under Dispersal by Birds (Chapter IV).

Willis and Burkill (in " Observations on the Flora of Pollard Willows near Cambridge," Cambridge Phil. Soc., viii, pt. ii, p. 82) give a list of plants growing in the tops of Pollard Willows in Cambridge. These include *Ranunculus acris*, *R. bulbosus*, *R. ficaria*, *Barbarea vulgaris*, *Sisymbrium alliaria*, *Cerastium tetrandrum*, and *C. triviale*, *Stellaria media*, *Geranium Robertianum*, *Rhamnus catharticus* (birds), *Acer pseudoplatanus* (wind), *Lathyrus pratensis*, *Prunus cerasus* (birds), *Rubus idaeus*, *R. rusticus*, *R. corylifolius* (birds), *Geum urbanum* (adhesive), *Rosa canina* (birds), *Pyrus aucuparia* (birds), *Crataegus oxyacantha* (birds), *Ribes grossularia*, *R. nigrum*, *R. rubrum* (birds), *Epilobium hirsutum* and *E. parviflorum* (wind), *Bryonia dioica* (birds), *Chaerophyllum temulum* (wind), *Anthriscus sylvestris* (wind), *Heracleum spondylium* (wind), *Hedera helix* (birds), *Sambucus nigra* (birds), *Viburnum opulus* (birds), *Lonicera periclymenum* (birds), *Galium mollugo*, *G. aparine* (birds probably), *Senecio Jacobaea* and *S. aquatica*, *Achillaea millefolium*, *Leontodon hispidum*, *Lactuca muralis*, *Cnicus lanceolatus*, *Fraxinus excelsior* (wind), *Syringa vulgaris* (wind), *Calystegia sepium*, *Solanum dulcamara* (birds), *Veronica hederaefolia*, *V. chamaedrys* (wind), *Nepeta glechoma* (*Glechoma hederacea*) (ant-dispersed), *Stachys sylvatica*, *Lamium purpureum*, *L. album* (ant-dispersed), *Plantago major*, *Polygonum aviculare*, *Rumex crispus*, *R. obtusifolius*, *R. acetosa* (wind-dispersed), *Ulmus campestris* (wind-dispersed), *Humulus lupulus* (wind-dispersed), *Urtica dioica* (adhesive), *Alnus glutinosa* (wind-dispersed), *Asparagus* (birds), *Phleum pratense*, *Deschampsia caespitosa*, *Holcus lanatus*, *Avena pubescens*, *Cynosurus cristatus*, *Dactylis glomerata*, *Poa annua*, *P. pratensis*, *P. trivialis*, *P. nemoralis*, *Lolium perenne*, *Festuca ovina*, *F. elatior*, *Bromus mollis*, *Brachypodium sylvaticum* (all these grasses by wind or in birds' nests).

Comparing this list with that of Thomas, we see that the lists are almost identical, though the Cambridge flora is more extensive, probably from the larger number of trees examined. Hardly a plant from Thomas's list is missing from that of Willis. *Chelidonium majus* and *Humulus* are the only ones missing, and *Lonicera periclymenum* is replaced by *L. xylosteum* in Thomas's list, which might be expected. Practically all the drupe and berry plants common in the districts are carried by the birds to these pollarded trees, which are so convenient for nests.

H. S. Thompson (in *Nature*, cxvi, 710, under the title of "Flowering Plants as Epiphytes in Willows and Alder") gives an account of plants thus found by him on the banks of the River Chew, between Bath and Bristol. He found 103 species, but does not give a complete list. However, out of his paper I extract what species he has recorded, and arrange them under dispersal methods.

BIRD-DISPERSED, baccate and drupaceous: *Rosa*, *Hedera*, *Prunus spinosa*, *Crataegus*, *Ribes grossularia*, *Sambucus*, *Solanum dulcamara*, *Adoxa moschatellina*.

ADHESIVE: *Geum urbanum*, *Bidens tripartita*, *Ranunculus repens*, R. *auricomus*.

WIND-DISPERSED: *Petasites*, *Tussilago farfara*, *Deschampsia caespitosa*, *Anthriscus sylvestris*, *Ulmus*, *Cirsium*, *Eriophorum*, *Lactuca muralis*, *Fraxinus*, *Eupatorium cannabinum*, *Valeriana officinalis*.

FLOATING SEEDS OR SEEDLINGS (perhaps brought by flood): *Ranunculus ficaria* (probably by bulbils), *Nasturtium officinale* (not known in the district), *Alnus*, *Angelica*, *Lythrum*, *Thalictrum flavum*, *Spiraea Ulmaria*, *Lysimachia vulgaris* (not known in district), *Juncus bufonius*, *Scrophularia nodosa* (perhaps as seedlings).

TRANSPORTED BY ANTS: *Symphytum*, *Viola Riviniana*, *Nepeta Glechoma*, *Prunella vulgaris*, *Ajuga reptans*, *Stellaria media* var. *neglecta*, *Luzula campestris*.

DUBIOUS (perhaps by ants or wind): *Arenaria trinervia*, *Conium*, *Stachys sylvatica*, *Geranium pratense* and *G. Robertianum* (perhaps by explosion), *Dipsacus*, *Verbascum*, *Brassica Rapa*, *Barbarea vulgaris*, *Stellaria aquatica*, *Lychnis dioica*, *L. floscuculi*, *Galium cruciatum*. Some of these may have been carried up by birds in nest building. Many, e.g. *Scrophularia* and *Verbascum*, etc., often occur on walls on to which the seeds have been blown.

J. Holmboe (in "Studies of the Vegetation of Cyprus") gives some account of the plants growing there epiphytically on trees. These are the following (I separate them according to dispersal methods):—

BIRD-DISPERSED: *Smilax aspera* (on *Quercus lusitanica*), *Morus alba* and *Ficus carica* (on many trees), *Olea europea* (on *Ceratonia*).

WIND-DISPERSED (probably): *Avena sativa* (on *Ceratonia*), *Bosia cypria* (on *Olea*), *Arabis purpurea* (on *Platanus*, 9 feet from the ground), *Ferula communis* on *Ceratonia* (5 feet from the ground), *Prasia majus* (7 feet from the ground). The nucules of this *Labiate* may have been carried by ants, but we find several *Labiates*, *Lamium*, *Nepeta*, etc., constantly on trees and walls, apparently wind-dispersed as well.

FLIGHT OF ACHENES BY ICE FILAMENTS.

Here I may call attention to a very curious method of flight of achenes described by A. F. Foerste (in *Bot. Gaz.*, vii, 40, 1882). The achenes are those of the small Composite *Ambrosia trifida* in Arctic America. Foerste says that the achenes are beaked, and possess five protuberances at the base, and that in winter five or six strands of ice are attached to these on frosty mornings, and as these ice-curls are from 1½ to 3 inches long, he suggests that they may aid in the flight of the achenes. This is quite likely, but such a way of utilising the winds for dissemination must be very unusual. It serves, however, to show in what strange ways dispersal may be effected.

WIND-DISPERSAL OF INFRUCTESCENCE OR OF WHOLE PLANTS.

Besides the dispersal by wind of plants and seeds specially adapted for flight, we have a number of cases in which either the whole heads of fruits or the whole plant may be rolled or driven along open country, scattering the seeds as they go. Here there is no further modification than lightness.

of plant or head of fruits, and a ready detachability. The action is only available over flat plains, steppes or deserts, but it has effectuated the very wide continental spread of the plants. I have already mentioned the dispersal of fragments or whole plants bearing fruits, by whirlwinds, as described by Woodruffe-Peacock, and it is clear that branches with fruits may be occasionally carried for some miles by hurricanes. I here deal with the more specialised plants which are often or habitually dispersed in this way.

TUMBLE-WEEDS.

The plants known as tumble-weeds are those in which the whole infructescence, or a part of the plant, or the whole of it carrying the seed, is torn off by the wind and drifted along, releasing and distributing the seed as it goes. This kind of dispersal is peculiar to deserts, steppes or prairies. The best known example is the Rose of Jericho, *Anastatica hierochuntica*, of the deserts of Asia Minor and Northern Africa. The plant is a small, rather woody crucifer, which, when fresh and damp, expands its branches, but when dry closes them over so as to form a ball. The plant remains closed during the long drought which follows the ripening of the fruits, small pear-shaped pods containing several seeds which in the dry state of the plant are enclosed in the round network of the branches. These balls or " roses " are blown along the desert by the wind till they reach a wet spot, or are wetted with rain, when the branches recurve and the ball opens, and at the same time the valves of the pod are opened and the seed is washed out by the rain and further dispersed (Pl. II, fig. 3).

Salsola Kali (*Chenopodiaceae*) is a rather stiff spreading herb with sharp pricked leaves, apparently originating in north temperate Europe and Asia, chiefly on the sea coasts and more or less saline flats. It has been accidentally introduced into America and Australia, where it is known as " Roly-poly " and " Russian thistle," and is recognised as a pestilential weed. In England it is usually a sea-coast plant, but appears inland as a ballast plant, and was growing on the Thames bank near Kew in 1926. It appears to have been introduced into America and Australia partly by ballast and partly in cereal seed, and then to have been spread by flood and river; but it is also blown and rolled about the American prairies and the Australian flats by wind (Davey and Maiden). In the southern and western areas it has been stated that it was introduced also by attachment to cattle from Europe, and it appeared in New Zealand in 1873 through cattle from Australia, where it had arrived before 1802. It is recorded from Tenimber Island and Timor in 1870, and New Guinea quite recently; in New Caledonia in 1865. In South Africa and America from the north to Argentina and Chile it is abundant. It occurs in a wild state in Europe and Central Asia to north India and China. In South Africa, H. G. Dittmer says, it spreads with enormous rapidity, killing out all plant life round it. Here it is carried about largely by river. Mr. Burtt-Davy writes that he has driven through a small forest of it at the mouth of one of the rivers in the Cape Province. Its dispersal by wind as a tumble-weed is, however, recorded by almost all writers in Africa, America and Australia. In the Proceedings of the Pan-Pacific Congress, Australia, 1893, it is said of the plant: " It forms round balls of light green in summer, dying in winter, " easily dislodged by wind, and then rolling along the plain, collecting as " they go, till stopped by a fence or other obstacle. In this position they lock " up quantities of drift sand; while rolling they deposit their seed." Kerner includes it as one of the plants of the Russian steppes which form large balls known as " wind-witches " or " steppe-witches " by the Russians. He writes:— " The herbaceous plants of the steppes of Southern Russia which exhibit

"the phenomenon of the decay of the bases of the stems in the fruiting season, "and a consequent liberation of the dry aerial portion of the plant belong to "families of the most various kinds. The most common are *Alhagi camelarum* "(*Leguminosae*), *Phlomis herba-venti* (*Labiatae*), *Centaurea diffusa* (*Compositae*), "*Rapistrum perenne* (*Cruciferae*) and *Salsola Kali*. It often happens that a number "of these dry, branching herbs get hooked and entangled together as they roll "along, until at length they form a ball as big as a cart-load of hay. Such balls "have been seen lifted up by whirlwinds and driven bounding over the plain."

M. A. Carleton ("Observations on the Plants of Oklahoma," Contrib. U.S.A. Nat. Herb., i, 223), says of *Cycloloma atriplicifolium* and *C. platyphyllum* (*Chenopodiaceae*) that specimens of these plants, 3 feet across, are blown along, and Clarke and Fletcher (in "Farm Weeds of Canada") give as tumble-weeds *Amaranthus blitum*, *A. albus* and *A. graecizans* (*Amarantaceae*), *Corispermum hyssopifolium* and *Axyris amarantoides* (*Chenopodiaceae*), *Solanum rostratum* (*Solanaceae*), both in America and in Australia, where it has been introduced, and *Echium vulgare* (*Boragineae*) introduced from Europe. F. W. Covills ("Botany of the Death Valley, California," Contrib. U.S.A. Nat. Herb., iv, "Dissemination of Species") says that in *Eriogonum trichopus* (*Polygonaceae*) the stem breaks off at the base and the whole plant is blown off over the desert as a tumble-weed.

Sisymbrium altissimum.—The tumbling mustard is a native of Europe which has been introduced into North America. When the seeds are ripe the whole head of the plant breaks off and is blown about the prairie, scattering the seeds far and wide. The seeds are not easily shed, and a head of this plant may blow about the prairie for a whole winter, dropping a few seeds at intervals for many weeks. ("Farm Weeds of Canada," G. H. Clarke and J. Fletcher.)

Odontospermum (*Asteriscus*) *pygmaeus* is a dwarf *Composita* which ranges from Syria to the Sahara, the achenes of which are dispersed by the rolling of the plant. When they are ripe, the leaves seem quite to disappear, the involucral bracts close over the fruits, and the plant, now quite withered, is blown away across the desert, and the involucre does not open till the rains set in and wash the fruits further along.

Morettia phileana (*Cruciferae*).—Grant (in Trans.Linn. Soc., xxix, p. 27) records that spheres of this plant in a withered state were found blowing about the desert and plain of Belama (Nubia).

Dr. Aitchison (in "The Botany of the Delimitation Commission," Trans. Linn. Soc., ii, vol. iii, p. 4) writes:—

"Peculiar-looking balls formed of a prickly fruited shrub, *Agriophyllum* "*latifolium* (*Chenopodiaceae*), with few or no leaves, were noticed rolling about "driven by the winds hither and thither over the flat clay plains, occasionally "accumulating into heaps. The shrub grows in loose sand, and as it is very "leafy it is easily lifted out of its position by the wind, and, being driven about, "it takes the form of a ball, which is increased in size by coming into contact "with similar plants. It was soon dubbed 'the wanderer.' The natives call "it the 'spinning wheel' in allusion to this peculiarity."

Psoralea argophylla (*P. esculenta*) (*Leguminosae*).—In this American herb a joint is formed in the stem very near the top of the ground, as is done in a leaf when detached from a branch. It cuts through all the tissues, so that when the top dries it is broken off readily by the wind and thus rolled across the prairie (J. E. Todd, *Bot. Gaz.*, viii, 231). This seems to be a more definite modification for tumble-weed dispersal than in most cases if, as Todd says, there is a specific line of growth of cells across the stem distinctly cutting it off from the base. R. Miller Christy, in an account of the flora of Manitoba, describes this tumble-weed in much the same way. He says: "By the time "the fruit is ripe, flowers, stalks and all become dry, brown, rigid. The plant

"separates just above the ground and is blown along; frequently dry plants "are found arrested and collected together in the wagon-tracks of the settlers." The plants, he shows from a comparison of five specimens, average 6·6 inches tall, and when dry have an average weight of 30·4 grains each.

Wellstaedtia.—A genus of two known species, one *W. socotrana*, found in Socotra, the other *W. dinteri*, near the Great Fish River, are tufted woody plants with dense heads of stiff leaves, small flowers and very small capsules of a two-celled ovary containing a single hairy seed in one of the cells. It is referred to the order *Boraginaceae*, though the structure of the fruit is quite anomalous. The whole plant, with its woody root when dry, is apparently blown out of the sand and whirled along, after the style of *Anastatica*. Somewhat similar is the behaviour of *Fedia* (*Valerianella*) *cornucopiae* (*Valerianaceae*).

Plantago cretica is an annual plant of Crete, Rhodes, Asia Minor and Syria. It has a short taproot, with a tuft of flowering stems. When the fruit ripens the stems curve down to the outer side of the plant and force the taproot out of the ground, so that the whole plant is detached in the form of a flattened ball, and, being very light, is blown along by the wind.

Gundelia Tournefortii (*Compositae*) grows in loose, round, prickly sods, with a long taproot, the top of which rots away when the fruit is ripe, and the sod rests on the plain loose, and is readily blown along by the wind. It is a native of Persia.

Even in England we have some cases of tumble-weeds. Dymes (in Ealing Nat. Hist. Soc., 1901, 38) says that whole branches of Sea-Campion (*Silene maritima*) bearing capsules may be seen blown away by wind, aided by the bladdery calyx, which acts as a balloon, and he says, too, of the house-leek (*Sempervivum tectorum*), that in its native home on mountainous rocky ledges in the Alps the almost globular offsets are blown and roll from ledge to ledge. After a violent gale in October, 1927, I saw a torn-up fruiting plant, withered, of *Lunaria biennis*, blown to some yards distance. It might easily have been carried to a much greater distance had the ground been open. *Thlaspi arvense* also appears sometimes to be torn up and blown, with its pods on, to some distance.

There are several species of *Selaginella* (*Lycopodiaceae*), which form rosettes of branches, and when the dry season comes on, curl up into ball-like masses which are driven along by wind. These are all natives of the deserts of Texas, Mexico and Costa Rica. When the rains begin these plants take on a green colour again and are revived. The species which behave thus are *S. pringlei*, *S. lepidophylla* and *S. cuspidata*.

Bulbils Dispersed by Wind.

Here we may introduce some cases of bulbiliferous plants of which the bulbils are blown away from the plant. One of these is *Poa alpina* of the mountains of Scotland, Yorkshire, and the European alps. Here the seeds are replaced by bulbils with long grassy points. Massart says that these bulbils are dispersed by wind in the Alps.

Remusatia Hookeriana and *Gonatanthus sarmentosus* (*Araceae*) are also mainly reproduced by bulbils which, being very light, are probably dispersed by wind. They are natives of the mountains of North India, and *Gonatanthus* occurs also in Siam, where it is said to be an epiphyte. The bulbils are borne on long branched, erect shoots, often in a dense mass. They are about a quarter of an inch long, of many bracts, lanceolate, and ending in a thin papery linear flat point, by which they can readily be blown away with the wind. (R. *vivipara* has these points in the form of stiff hooked spines, and is evidently bird-dispersed.)

INFRUCTESCENCE DETACHED AND DISPERSED BY WIND.

In a number of plants in open desert regions and sand-hills the whole head of infructescence is detached and is blown along, rolling over and over as it goes and scattering the seeds in its passage.

Among these is the beautiful *Amaryllidaceous* plant, *Buphane toxicaria*, a native of the South African deserts. It possesses a very large head of brilliant red flowers, which are succeeded by a large umbel of capsules. This, Mr. Burtt-Davy tells me, when the fruit is ripe, is detached and blown along the sandy desert, rolling along in the wind and scattering its seed so effectually that the plants are always found distinct from each other.

Kerner thus describes the dispersal of *Paronychia kapella* (*Paronychiaceae*), a small plant of wide distribution in the region of the Black Sea. The fruits are brought to maturity in the height of the summer season, and are then surrounded by white, silvery, membranous bracts. When the season for dispersal has arrived, the entire tuft of fruits in the form of a small glomerule is detached and lies lightly on the ground where the least puff of wind imparts to it a swift rolling motion. Sometimes if the ground is uneven the rolling is converted into a hopping or springing motion, and occasionally such masses of fruit are raised by powerful gusts of wind and carried considerable distances through the air.

Several species of Clover (*Trifolium globosum*, *T. subterraneum* and *T. nidificum*) are disseminated in much the same way. In the heads of flowers borne on the end of the peduncle only a few are perfectly developed, while a number of abortive flowers are crowded together in a tuft in the centre of the head. When the fruits are ripe, the calyx teeth of the abortive flowers increase in size and become long hairy bristles which bend over and form a globular network over the head of pods. The head then breaks off and is rolled away over the downs by the wind.

Kerner mentions the spirally curled fruits of *Medicago scutellata*, which are detached from the plant when ripe and rolled along the ground by every puff of wind. Most of the *Medicagos* have their spiral fruits armed with hooked spikes with which they adhere to passing animals, but *M. scutellata* is quite smooth and could be easily rolled along.

Ruppia maritima.—In a note in Kew Herbarium T. Kirk gives an account of a curious method of wind dispersal of this world-wide aquatic plant. He writes :—

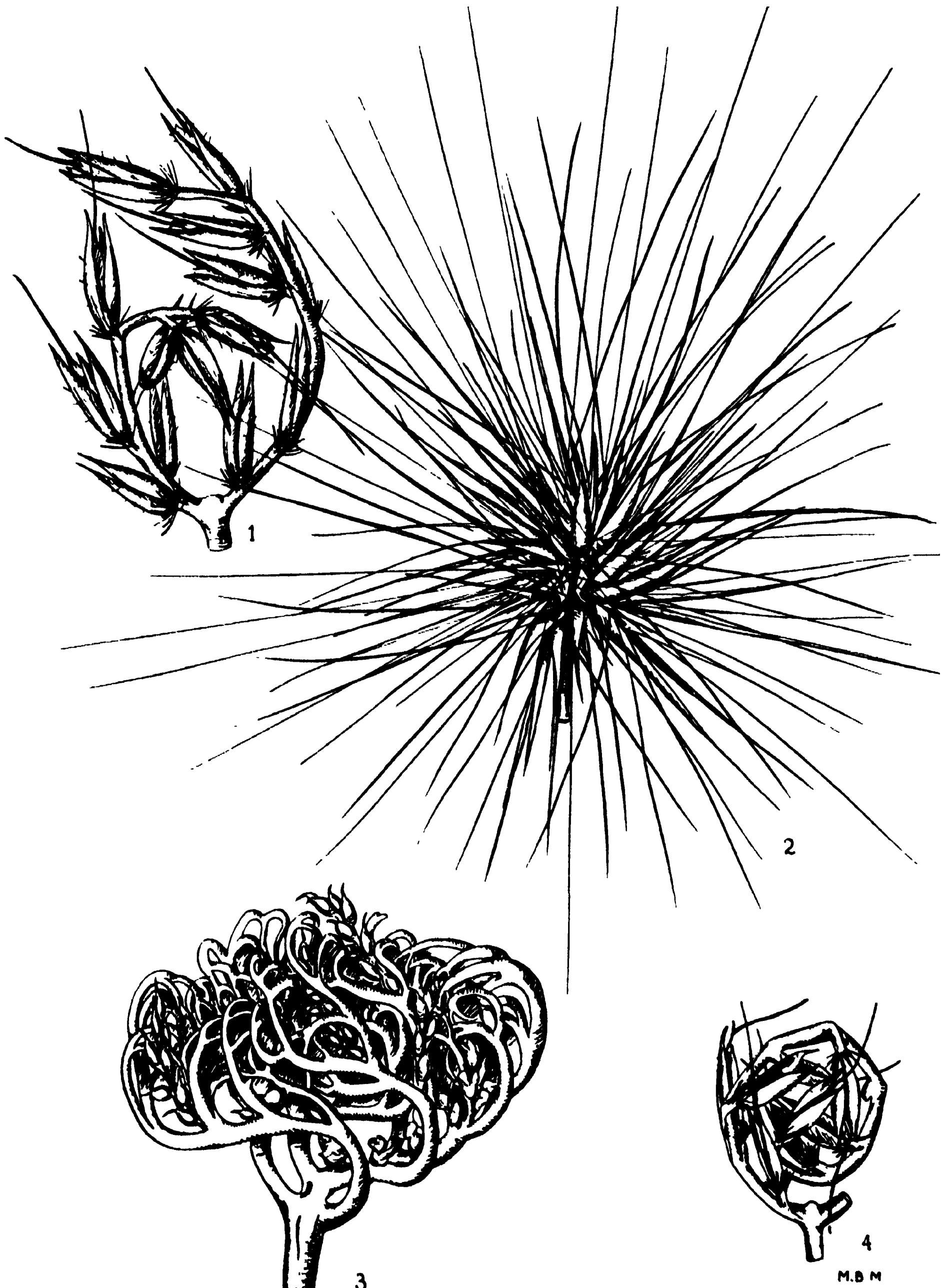
> " It appears that when the peduncle is detached the fruits become subject " to the action of wind and wave, and are washed ashore, probably mixed " with green algae, which, together with the decaying outer layer of the pericarp, " causes a certain amount of adhesiveness, so that when rolled along the shore " by the wind they form sausage-like or round masses, the fruits being so " compacted together that it is difficult to extract single specimens."

The rough points on the crustaceous pericarp and the slightly scabrid flexuous peduncles would facilitate this process. Hector says also that on Lake Ellesmere, Canterbury, New Zealand, the peduncles form large balls. The plant growing in such masses as it does in New Zealand might readily be blown in this manner across open spaces from lake to lake or creek to creek.

In *Zinnia grandiflora* (*Compositae*), a native of Colorado, the ray-florets become dry and rigid, persisting after the achenes are ripe. Then the whole flower-head becomes detached and is blown across the plains, the stiff ray-florets acting as wings (D. F. Day, *Bot. Gaz.*, ix, 29).

Bessey also describes another form in which the head of a *Composita*, or, rather, the whole mass of fruits, is blown away, tumbling over the deserts

PLATE II.



WIND-DISPERSAL. TUMBLE-WEEDS.

FIG. 1.—*Dimeria Woodrowii* (raceme unfurled, enlarged, after Stapf).
,, 2.—*Spinifex squarrosus* (head of spikelets, reduced).
,, 3.—*Anastatica hierochuntica* (whole plant).
,, 4.—*Dimeria Woodrowii* (raceme closed, enlarged).

[*To face p.* 36.

of Western America. *Townsendia sericea* is a small herb in which, when the achenes are ripe, the involucre, which was previously expanded, closes over the head of fruits and, contracting, forces out the whole as one mass rather suddenly. The achenes have an abundant pappus, the hairs of which are hooked with double recurved points, and on drying and twisting entangle each other so as to form a compact body of an ellipsoid form. This extruded mass is then blown away by the wind, gradually breaking up as it goes, dispersing the achenes. When it breaks in two, each part continues its course, the pappus hairs expanding make the two halves into ball-shaped bodies. In this way the seeds are strewn over a large area.

In some grasses inhabiting open sandy plains the fruiting panicle becomes detached and is blown along by the wind, scattering the grains as it goes. Such are *Aristida setacea* and *Panicum obscurans* Stapf (*Isachne obscurans* Woodrow), which are natives of the dry country of the Deccan, India. Prof. G. Marshall Woodrow thus describes them (in *The Gardeners' Chronicle*, 1898, i, 161):—

"Of the *Gramineae*, the most frequent one, *Aristida setacea* Retz., was "in seed, and the manner in which it distributed its seeds is very interesting. "Its three-branched awns twist together in such a manner that a perfect sphere "is formed by their extended points, and the balls roll hither and thither in "every breeze; one would appear at the door of the tent like a shy stranger, "uncertain whether to advance or retreat, a puff would drive it in a foot, "another would send it out again, a third would make it roll straight to one's "feet. Another grass of interest is *Isachne obscurans* (referred later by Dr. Stapf "to the genus *Panicum*), remarkable for its habit of letting loose its entire "inflorescence, a large open panicle of most elegant form, which is rolled about "by the wind till it is caught in some bush."

Aristida setacea is a native of Madagascar and Ceylon, as well as the plains of India. It has a dense spike of spikelets, of which all three glumes are armed with long scabrid awns, the first two having one, the third (which is convolute and includes the grain) having three awns.

Panicum obscurans is about 18 inches tall, with a very lax, scabrid spreading panicle bearing scattered spikelets. Mr. Burtt-Davy tells me it behaves, in the Transvaal where it has been introduced, in the same way as Prof. Woodrow describes it.

Another grass which is apparently distributed in a similar manner is *Dimeria Woodrowii* Stapf, a little annual grass occurring in Southern Bombay. It is 3 to 6 inches tall, and bears two spikes of spikelets, each ½ to 1 inch long. At first they spread apart as in the other species of the genus, but when the fruit is ripe the spikes curl up together, forming a small ball of eight spikelets on each spike, these bearing an awn which projects from the ball. A figure of this curious little plant is given in the Icones Plantarum 2312, from which I take the figure (Pl. II, figs. 1 and 4).

In such genera as *Hordeum* the raceme breaks up into joints bearing the seed enclosed in a number of persistent bracts or glumes, and these joints are blown along the ground and up to some height by the wind, as is mentioned under the section dealing with Glume Wings (p. 99).

The most striking of all wind-dispersed grasses is the porcupine grass (*Spinifex squarrosus*), an inhabitant of sandy seashores through the Malay Archipelago, and on the coast of the Malay Peninsula to Ceylon and India, Siam, Formosa and China. The remaining three or four species of the genus inhabit the seashores of Australia, in which country there is no doubt that the *Spinifex* was first evolved. The most closely allied species to *S. squarrosus* is *S. longifolius*, but owing to the greater slenderness and weakness of the bracts

of this species, it has failed to spread over the great area occupied by *S. squarrosus*. The female head of spikelets is round, with long radiating spikes, each bearing one spikelet, with long slender bracts ending in spines, the whole forming a very light globose ball of glumaceous spikes, 10 to 12 inches through. When in fruit the ball is detached with the upper peduncle, and is blown along the sand at a surprising rate. The balls run on the tips of the spines, which project in all directions, and frequently bound into the air (Pl. II, fig. 2). My fox-terrier, thinking they were some live animals, gave chase to them and pursued them as fast as she could run, but had great difficulty in overtaking them. Dr. Trimen states that they are assisted in their progress by the elasticity of the peduncle, and that as they run rolling over and over they drop the seeds in transit. "One may be followed by the eye for miles on its journey," he says, and adds that they are so buoyant as to float lightly on the water, when the upper peduncles, acting as sails, transport them across estuaries ("Flora of Ceylon," v, 175). I have never seen the heads floating at any distance from the coast, but it is quite possible that they can drift or sail for some way on the usually quiet seas of the Malay region. The plant had reached the island of Krakatau and the adjacent islands (after the flora was destroyed by volcanic action in 1883) by the year 1896, and it occurs in many of the islands of the Malay seas, and must have crossed considerable tracts of sea to have reached Formosa, Ceylon, etc. It is found in the Laccadives 120 miles from the coast of India, and the Maldives, 300 miles from Cape Comorin and 400 miles from Ceylon.

Besides these, a number of other grasses in open desert regions are dispersed by their inflorescences being blown along as tumble-weeds. This seems to be the most common in the North American deserts. In many cases the peduncle of the panicle is drawn out of the upper sheath of the grass as in *Panicum capillare*. In this the main axis may grow to a length of 2 feet or more, after flowering, and often becoming loosely spiral (Hitchcock).

In *Elymus elymoides* the spike separates and becomes light enough to be blown along from the spreading of the long awns. In *Eragrostis pectinacea* and *E. refracta* the whole panicle breaks off near the base of the culm and rolls along the ground, its progress being facilitated by the horizontally spreading branches which act as sails. The breaking off of the panicle is effected by the slenderness of the lower internodes (J. H. Kearney, "Botanical Survey of Dismal Swamp," Contrib. U.S.A. Nat. Herb., v, 6, 1901).

Other American grasses dispersed in this way are *Schedonnardus paniculatus*, *Chloris verticillata* (J. Adams), *Agrostis scabra* (Dewey).

Maiden states that in Australia heads of *Deyeuxia Forsteri* are broken off and blown along the deserts.

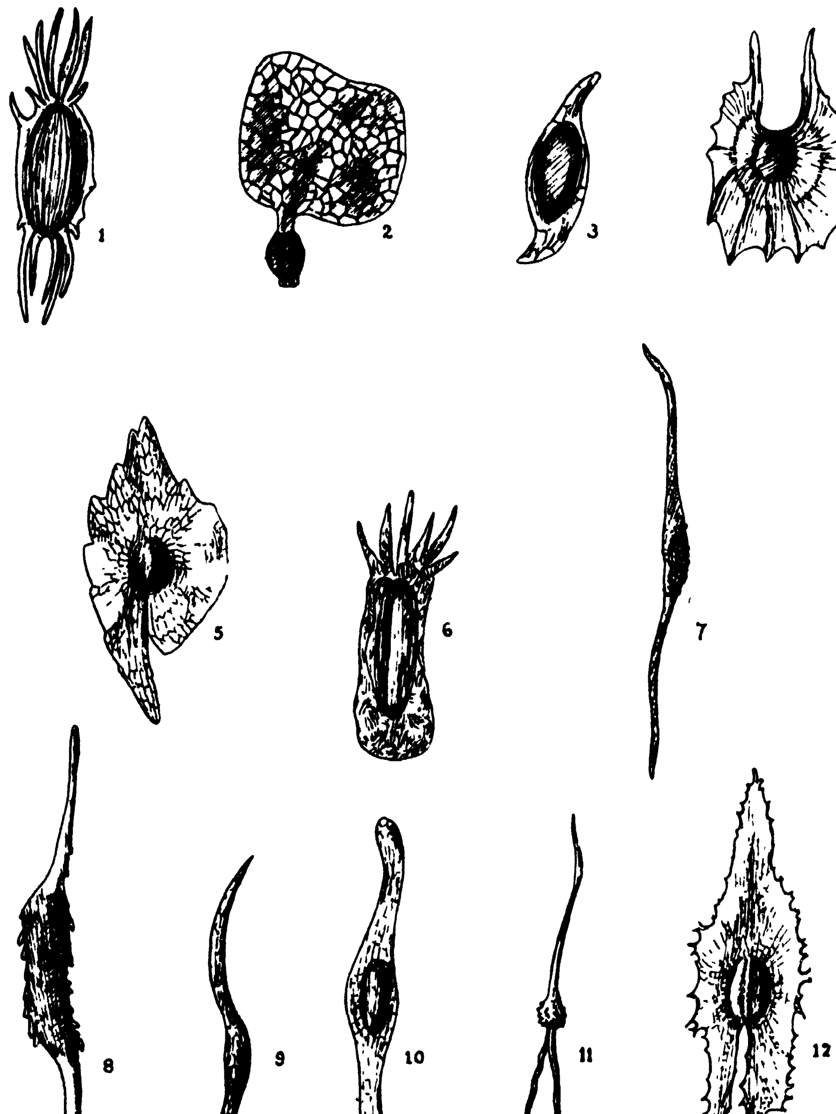
In *Agrostis scabra* (*A. laxiflora*) R. Miller Christy (in "Notes on the Flora of Manitoba") says that the heads break off in August at one of the joints of the stalk, and are blown about by the wind, and he has seen them stuck in hedges and bushes where they have been blown.

DUST-SEED.

Dust- or powder-seed is the name given to very light seed which possesses no special apparatus for wind-dispersal except a large evolution of a very thin testa in proportion to the actual weight of the nucleus. (I formerly included under this head the spores of Cryptogamic plants, but it is more convenient to discuss these separately under the head of SPORES, *see* p. 50).

The dust-seed is the lightest form of seed of any flowering plant. It is readily borne away by the wind and can drift about in the air, sometimes ascending to very great altitudes, until sooner or later it comes to rest, and if

PLATE III.



WIND-DISPERSAL DUST SEEDS AND SMALL WINGED SEEDS.

FIG. 1.—Seed of *Rhododendron ponticum* (much enlarged).
„ 2.— „ „ *Pterospora Andromeda.*
„ 3.— „ „ *Dendrobium crumenatum.*
„ 4.— „ „ *Galeola Ledgeriana.*
„ 5.— „ „ *G. Lindleyana.*
„ 6.— „ „ *Rhododendron luteum.*
„ 7.— „ „ *Nepenthes Rafflesiana.*
„ 8.— „ „ *Aeschynanthus rhododendron.*
„ 9.— „ „ *Buddleia variabilis.*
„ 10.— „ „ *Spathoglottis plicata.*
„ 11.— „ „ *Uncaria sclerophylla.*
„ 12.— „ „ *Hymenodictyon excelsum.*

[*To face p.* 39.

in a suitable locality, can germinate and grow. There are many intermediate stages between the winged seed, with the finely drawn out testa, such as those of *Uncaria*, and the lighter and more minute seed of the Orchids, but the extreme difference of the weight makes the whole difference in the matter of dissemination, for next to the spores of Cryptogams these minute dust-seeds are the furthest disseminated of any kinds of plants, by the action of wind. Thus whereas no winged seed plants reach distant oceanic islands, it will be seen that dust-seed plants can, and do so.

Most of the dust-seed plants belong to the *Orchidaceae* (Pl. III, figs. 3 and 10), but many of the *Apostasiaceae* have like seeds, and very similar are the small seeds of *Sarracenia*, *Nepenthes*, etc., which, however, have the testa more distinctly drawn out into wings or hair-like processes. Included among this class of plants may be the species of *Balanophora*, belonging to the yellow unisexual group. In these the whole fruit is minute with a thin pericarp. They are, as far as I know, the smallest fruits of any flowering plant, and are blown away like dust with the slightest breeze. The plants are small yellow, almost leafless parasites about 3 inches tall, growing apparently on the roots of one or more species of *Ficus*. All, or nearly all, are island plants occurring in the South Asiatic islands from Tahiti to the Comoro islands. *Balanophora Hildebrandtii* is said to occur in both these localities, *B. Micholitzii* in Timor Laut, *B. Zollingeri* in Salayer Island, *B. alutacea* in Java, and *B. insularis* in Christmas Island and Pulau Aur off the coast of Johor, 850 miles apart. In preserving specimens of the latter plant I was much struck with the way the minute fruits drifted away on the high breezes, like the pollen of a conifer. They were produced in great abundance on the little plant and borne on short stalks. The plants, which were very scanty, grew in open woods or between high rocks. The other species of the genus grow in dense forest in wet spots, their fruits are not so small and are apparently diffused mainly by rain-wash. These are quite absent from any islands.

The *Apostasiaceae* are a small group of terrestrial plants with capsules like those of *Orchidaceae*, which dehisce and release a large number of small seeds with a loose testa very much in the same way as Orchids, except one species, *Neuwiedia Curtisii*, which has baccate fruit of a bright red colour and small round black seeds. They are natives of thick forests in the Malay Peninsula and islands, but are quite absent from oceanic islets. There are two genera, *Apostasia* and *Neuwiedia*. The former has small linear capsules opening by a longitudinal slit on one side. In the latter the triquetrous capsule opens into 3 valves. The seeds are very small and resemble those of the *Vanilla*, the nucleus being covered with a firm reticulate testa, not loose and expanded, as in Orchids, and consequently not so light. The *Apostasias* range from India to China, Siam, the Malay Peninsula and islands, *Neuwiedia* from Burma to the Malay Peninsula and islands to New Guinea. The distribution, it will be noted, covers a very much smaller area than does that of the capsular Orchids and even than *Vanilla*, which is spread over Africa, tropical Asia, and South America, but that genus owes its widely extended area to the aid given by birds which eat the pulpy fruit and distribute the seeds.

ORCHIDACEAE.

The Orchids, except *Vanilla*, have capsular 3-valved fruits which dehisce in various ways. In some plants the capsule splits into 3 or 6 lateral slits, both ends of the valves remaining attached at the top and bottom, so that the seeds are ejected or blown out through the slits. This is the most common method of dehiscence, and is seen in *Orchis*, *Phaius*, *Odontoglossum*, *Ansellia*, and many other genera.

In some genera there are only two slits formed. In *Pleurothallis*, *Bulbophyllum*, *Angraecum*, *Epidendrum*, and in some species of *Angraecum*, the capsules open only by one split in one valve. *Dilochia* has a peculiar dehiscence, for the pendulous globose capsule only splits a short way on each face and not completely to the ends, somewhat similar to the dehiscence of some of the capsules in *Campanula*.

In the group *Sarcantheae* it is usual for the capsule to split on one side only, longitudinally for its whole length. In a few genera the capsule splits at the top and the valves recurve (*Leptotes*, *Maxillaria*, *Eulophia*, *Fernandezia*). In *Galeola* the long slender capsule splits into two narrow valves for its whole length.

In *Cattleya* the valve edges, after splitting, are connected with a network of fibres, so that the seeds can only be dispersed a few at a time through the meshes of the net.

In many cases there are, on the inner face of the valves, special expulsive hairs which move about when there is an alteration of humidity in the air. In ripe fruit these hairs, which are strongly hygroscopic, are detached from the base and act much as do the elaters of Liverworts (*Hepaticae*). On breathing on these hairs, which are mixed with the seeds, they immediately begin to move and aid in ejecting the seed. As a rule, and in the great majority of cases, whether the flowers when open are erect, horizontal, or deflexed, the capsules in terrestrial Orchids are erect when they dehisce, and in epiphytic species are pendulous or more or less horizontal. Thus in the terrestrial species of *Liparis* the capsules are erect and usually appressed to the rachis, while in the epiphytic species they hang downwards ; and the same is the case in the epiphytic species of *Cymbidium*, the capsules are all pendent, while in those of the terrestrial *C. lancifolium* and some others the capsules when ripe stand erect.

In the terrestrial *Ophrydeae* and most of the small *Neottiae*, as well as *Microstylis*, *Plocoglottis*, *Thunia*, *Arundina*, *Bletilla*, *Anthogonium*, *Bromheadia palustris*, *Pteroglossaspis*, *Sobralia*, *Corymbis* and *Cypripedium*, which are all terrestrial plants, the capsules when ripe are erect. There are, however, a few terrestrial Orchids in which the capsules are deflexed or more or less horizontal when ripe. In *Tainia*, *Nephelaphyllum* and *Galeola*, some species have erect, others pendulous capsules. *Galeola* is a saprophytic leafless plant of which the stem is usually very long, straggling and branched, and often climbs to a considerable height over the roofs of cottages or upon trees. In these the capsule is pendulous, but the dwarf species (*G. javanica*), which is only about 6 inches tall, has horizontal capsules.

In the terrestrial genera *Phaius*, *Eulophia*, *Lissochilus*, *Acrolophia*, *Govenia*, *Spathoglottis*, *Epipactis*, *Geodorum*, however, the capsules so far as I have seen are pendulous. Most of these plants are inhabitants of open grassy countries or open woods, unlike many of the other species which inhabit dense forest. *Geodorum*, it may be mentioned, has a decurved raceme, so that it would not be practical for it to have erect capsules.

Many of the epiphytic species in high mountain districts grow on rocks and not on trees, but retain their pendulous capsules.

Dilochia Cantleyi, which always grows on high mountain rocks, has pendulous capsules, but the rare *D. Wallichii* is said to grow on trees, and I have little doubt that *D. Cantleyi* was originally epiphytic, though it never grows epiphytically now.

Bromheadia palustris, a plant of open grassy fields, although it belongs to an epiphytic genus, all of which (except it and another terrestrial species, *B. sylvestris*) possess pendulous capsules, bears its fruit quite erect, in spite of its having itself been originally epiphytic, still retaining the characteristic velamen on its roots, which occurs otherwise only in the epiphytic Orchids (Groom, *Ann. Bot.*, vii, 150).

The object of this difference between the position of the ripe capsule in epiphytes and terrestrial plants is clear. If the seeds of epiphytes on the summit of lofty trees were blown upwards, they would be floated clear of the trees on which alone they can grow. Falling at first as they do from a pendulous capsule, they may either come to rest on lower branches, or drift by the light airs of the forest through the mass of branches which forms the lofty covering of the forest, and germinate successfully there. In terrestrial species, especially in those with short pedicels, if the fruit were deflexed there would be a risk in dehiscence of all the seed falling in a pile at the base, and it is not I think probable that these minute light seeds would derive any benefit in dispersal from rain-wash. It is essential that the capsules should stand erect so that the wind may carry the seeds up and away from the parent plant. We see the same erection of the capsules before dehiscence in *Liliaceae*, and many other tall terrestrial herbs.

In the case of the comparatively few terrestrial Orchids in which the capsule is pendulous, we find that the plants are usually tall and the pedicels long, and that the plants generally grow in open country, so that the capsules 2 feet or more from the ground are swayed about by the wind and the seed is blown far away from the parent.

In epiphytic Orchids the capsule is pendulous, the pedicel often lengthening. In cases where the flowers are in dense racemes with very short pedicels, such as *Eria floribunda*, the capsules, which are linear in outline, project at right angles to the rachis, horizontally, in fact, but as the racemes are lateral on the erect stem, the seeds in dehiscence are blown horizontally so as to come into contact with the branches of neighbouring trees. In *Taeniophyllum*, small leafless and almost stemless epiphytes, the capsules of necessity stand erect, or in long-peduncled species lie horizontal. In fruiting, the pedicel frequently lengthens to a certain extent, especially in pendulous capsules and where the flowers are crowded together. In *Oberonia*, in which the crowded minute flowers are borne on very short pedicels so that all tend to form an almost solid block, the pedicels of the successfully fertilised flowers elongate, and serve to hold the pendulous capsule free of the dense flower-spike, and in most Orchids the pedicels elongate similarly during the development of the capsule. But this is carried out to a much greater extent in the case of two terrestrial Neottiaceous plants, *Corysanthes* and *Didymoplexis*. *Corysanthes* is a tiny plant, the stem of which is usually not more than 1 inch long, and bears a single cordate leaf and a subsessile flower large for the size of the plant. It grows usually imbedded in moss up to the leaf, so that the ovary in the flower is almost beneath the moss. In fruiting, the pedicel, soft and fleshy, develops to nearly 1 inch in length above the leaf and bears the oblong capsule at the top well above the surface of the moss. Were it not for the elongation of the pedicel, the fruit would ripen beneath the moss and no dissemination would be possible. In *Didymoplexis* the elongation of the pedicel is even more exaggerated. The plant is a saprophytic, leafless, rather fleshy Orchid, with a stem about 4 to 12 inches long, bearing one or more racemes of a few flowers opening singly. When fertilised the pedicel, originally $\frac{1}{3}$ or $\frac{1}{4}$ inch long, grows to the surprising length of 6 to 12 inches, bearing an elliptic capsule at the tip containing a great abundance of very light seed. The pedicels, which are much longer than the rest of the plant, are very fleshy and brittle. *Didymoplexis* grows in dense, dark forest, the short stem being imbedded in the dead leaves of the forest. There are several species closely allied ranging from India through the Malay regions to Fiji. It is interesting to note that this was one of the few terrestrial Orchids found in Christmas Island, 194 miles from Java, which is the nearest land it could have come from. The plant, growing in dense forest with trees usually 150 feet tall or more, over it, sheds its seeds, which

must be carried upwards through the leafy canopy and drifted through the air till by some chance one or more may fall on this distant and isolated island.

An allied plant is *Auxopus Kameruniana*, of West Africa, a slender, leafless herb, 6 inches tall. The flowers are very small, with a pedicel under 0·1 inches long, which lengthens in fruit to 1 inch. The capsules are rather numerous and seem to project horizontally rather than erect.

In most of the insect-fertilised Orchid flowers only a small percentage of them develop into fruits, at least in the epiphytic species. Thus *Dendrobium crumenatum*, the well known Pigeon-Orchid of the Malay region, blossoms approximately every nine weeks. All the flowers in any given locality open simultaneously on one day at dawn and remain open till the evening, when they wither. So abundant and floriferous was this plant on roadside trees in Singapore that the trees were white with the flowers on the day of blossoming. They were pollinated by a hornet (*Vespa cincta*), but this insect was not sufficiently abundant to pollinate more than a few flowers before they withered, so that, when the capsules were ripe, only one here and there could be seen. Very many plants did not produce a single one. Yet this species is the commonest species of the genus in the lowland districts, ranging from Siam, through the Malay Peninsula and islands to Christmas Island, though, as I have seen plants floating green and fresh and apparently unharmed in the sea to the south-east of Singapore, it may have successfully reached the island by sea travel. Though the plant fruits poorly in proportion to its abundance of flowers, its seeds are probably produced in very large numbers.

The terrestrial Orchids seem to produce more fruit in proportion to the number of flowers than do the epiphytic ones, especially those with large flowers. This is probably due to the smaller, more crowded flowers being visited by small and abundant insects, such as *Diptera*, and to their lower position on the ground, where insects are more abundant; but this point has a more distinct relationship to the fertilisation of the plants than to their actual spread by seed, and need not be dilated on here. The self-fertilised Orchids, such as *Spathoglottis plicata* Lindl., produce a capsule for almost every flower. Thus on examining a number of specimens I find that one with 30 flowers bore 10 fruits; of 15 flowers of another, 12 had set fruit; of one with 18 flowers, all had set fruit; while of the insect-fertilised form from Java, of 15 flowers, only 6 or 7 had set.

In the insect-fertilised *Spathoglottis aurea*, of 23 flowers none had set, and of two specimens of 21 flowers, 3 and 5 respectively had set fruit.

The self-fertilisation of *S. plicata* is due to the suppression of the rostellum, so that the pollen masses slip into the stigma. This self-fertilised form is the most common, and is the only form in the Malay Peninsula, where it is certainly the commonest ground Orchid. The insect-fertilised form occurs through the islands to the Philippines, and was one of the first four Orchids to reach Krakatau after the eruption.

The insect-fertilised species, such as *Habenaria*, *Zeuxine*, *Orchis*, etc., constantly produce a full complement of capsules. Darwin ("Fertilisation of Orchids," chap. ix, 280) gives some account, from his own observations and from those of others, as to the frequency or rarity of fertilisation, and the abundance of the species *Ophrys apifera*, self-fertilised, with every flower producing a capsule, is not so numerous in individuals in some parts of the country as *O. muscifera*, which is imperfectly insect-fertilised and, comparatively, rarely fruits. However, *O. apifera* actually covers a larger area in Europe than *O. muscifera* does; I have myself found it in plenty in a newly made turf bank in Norfolk where no other Orchid was growing, but was unable to find it anywhere else in the neighbourhood.

Cheeseman states that in *Pterostylis trullifolia* much less than a quarter of

the flowers produce capsules, and *Acianthus sinclairii* produced 71 capsules out of 7 flowers, yet it is not more abundant than the *Pterostylis*.

Fitzgerald says that the self-fertilised *Thelymitra carnosa* is not so common as *Acianthus fornicatus*, which rarely sets seed, and that in Australia *Phaius grandifolius* produces a capsule for every flower, while *Calanthe veratrifolia* only occasionally produces a single one, yet *Phaius* is rare and *Calanthe* common. Now, both these plants are very widely distributed, and in Malacca the *Phaius* is almost invariably self-fertilised and sets fruit to all flowers, but it is sporadic where it occurs, while in Jamaica, where it has escaped from cultivation and run wild for many years, it occurs abundantly in large masses. This form is, however, not the self-fertilised form.

Calanthe veratrifolia fruits well in the Malay Peninsula, and is much more abundant than the *Phaius*, and, like most of the genus, occurs in large quantities together in suitable localities. A species of *Phaius* was one of the first Orchids to reach Krakatau. It appears, therefore, that it does not always follow, from the number of capsules and consequently seeds produced, that an Orchid should be widely distributed over an extensive area, but the fact that it is widely distributed is due rather to the seeds more readily finding a suitable spot for growing.

Many millions of Orchid seeds must be dispersed throughout the world by wind, but never find a suitable settling place and so perish. The seeds are very minute among the smallest of any flowering plant, and extremely light; thus of *Orchis maculata* it requires 15,000 to weigh a grain. They consist of an embryo surrounded by a very thin, loose reticulate testa, usually drawn out at each end, except in *Galeola*, saprophytic leafless plants from tropical Asia. In these the testa is spread out into a circular wing surrounding the embryo, and the whole seed is much larger than in other capsular Orchids. In *G. hydra* the seed is minute with a circular wing. In *G. Falconeri* the wing is oblong, pointed at one end and toothed at the other, somewhat resembling those of some species of *Rhododendron*. These are referred to again under "Winged Seed" (*see* p. 124). The weights of some Orchid seeds have been estimated. Kerner gives the following :—

Goodyera repens	0·000·002 gramme
Gymnadenia conopsea	0·000·008 „
Stanhopea maculata	0·000·003 „
Beccari gives :—	
Dendrobium attenuatum	0·000·028 „
„ „	0·000·565 „
Rolfe :—	
Cycnoches chlorochilum	0·000·0036 „
Wallace :—	
Orchis maculata	15,000 to a grain.

The number of seeds produced by an Orchid is enormous, as shown by the following table :—

Orchid.	No. of Capsules on a Plant.	No. of Seeds in a Capsule.	Total No. to a Plant.
Cephalanthera grandiflora	4	6,020	24,080 x
Orchis maculata . .	30	6,200	186,000 x
Acropera sp.	—	371,250	374,000,000 xx
Maxillaria sp.	6	1,756,440	10,586,640 xxx
Cynoches chlorochilum . .	1	3,770,000	3,770,000 xxxx

Darwin = x. Scott = xx. Fritz Muller = xxx. Rolfe = xxxx.

(Darwin, "Fertilisation of Orchids," p. 277; Rolfe, "Fruit of *Cycnoches chlorochilum*," *Kew Bull.*, 1909, 200.)

Of this immense number of seeds, far the largest number must perish, for, as Darwin shows, allowing each plant of *Orchis maculata* a space of 6 inches square, and making an allowance of 400 bad seeds in a capsule, one plant could cover an acre of ground, and the great-grandchildren of one plant the whole of the land surface of the globe.

Orchid Seed and its Mycorrhiza.

It is well known that Orchid seed depends, at least in large measure, for its powers of germination on the action of a mycorrhiza, a fungus which grows symbiotically on the roots or penetrates them. Saprophytes seem certainly to be dependent on mycorrhiza for nutrition. The question is of much importance in the matter of dispersal of Orchids to distant islands by seed, as it entails the previous existence there of the mycorrhizal fungus. At least one distinctly saprophytic Orchid has been found in an oceanic island, viz., *Didymoplexis pallens* in Christmas Island, and this plant must certainly owe its growth there to a mycorrhiza.

Oakes-Ames, in an article entitled "Capacity of Orchids to Survive in the Struggle for Existence" (*Orchid Rev.*, 1922, p. 229), deals with the difficulty of Orchid seeds travelling to some distance and finding the requisite mycorrhiza for the germination of the seed, instancing the Orchids recorded as appearing in Krakatau after the eruption and the consequent destruction of all vegetable life. Assuming the seeds to have been blown over from Java (25 miles), how did these seeds find the necessary mycorrhiza for germination? He affirms that the mycorrhiza is not universally distributed. The wide and easy distribution of Orchids, however, would seem to negative this.

Ramsbottom says (*Orchid Rev.*, 1923, p. 72) that mycorrhiza occurs independently of Orchids. It occurs in soil near Orchids and grows in pure culture. Oakes-Ames suggests that the seeds may fall from the capsules and be inoculated with the mycorrhiza on the ground, and then be blown with the mycorrhiza across the sea. But if the seed has fallen from the fruit among the roots of, say, *Cymbidium* (really an impossibility, as the fruits hang far below the plants), or in the deep grass surrounding plants of *Arundina* and *Spathoglottis*, how could they be blown up and out by the wind? The whole system of Orchid-seed dispersal with projecting capsules exposed to the full wind negatives the fall of the seed to the ground and its rising again on the wind.

In the case of *Didymoplexis*, of what use would be the peculiar long upward growth of the pedicel in fruiting if the seeds were intended to fall on the soil and rise again before they can start on their wanderings? and were the seeds of the epiphytic Orchids on the upper branches of a tree 180 feet tall to fall in the dense mass of foliage below in a tropical forest, they would not only be quite unable to reach the ground, but if they did could not possibly drift up again. Ernst suggests that the mycorrhiza was blown to Krakatau from Java in the form of minute sclerotia. Ramsbottom quotes from Ernst that the *Leguminosae* on Krakatau possessed the nitrogenous bacteria tubercles characteristic of them, and pertinently asks if the seedlings of *Leguminosae* were provided already with tubercles, and thus blown across to Krakatau. There seems no reason why the spores of the fungus producing the necessary mycorrhiza should not be blown over to the islands, and remain in a mycelium state in the soil or on the tree branches, before the arrival of the Orchid seeds. We are at present ignorant of the full life-history of the mycorrhizal fungi of Orchids, and as to what genus the adult form belongs. Noack (*Bot. Zeit.*, xlvii, 1889) gives as fungi supplying mycorrhiza to Pine, Beech and other trees, *Geaster*, *Agaricus*, *Cortinarius*, *Lactarius*, *Elaphomyces*, and Jance (*Ann. Bot.*

Buitenz., xiv) mentions *Clostridium* as a fungus which produces mycorrhiza and is also a free plant.

Few fungi were collected by the expeditions to Krakatau, but this does not exclude the possibility of there being a number present, but which were not in condition for collection at the time. There were:—one *Hygrophorus* and two *Polysticti.* In Christmas Island fifty species have been collected, many of which are terrestrial fungi, and among them was a species of *Geaster*, a genus mentioned by Noack as supplying a mycorrhiza. All but eight of these fungi were collected by me in a month, and doubtless represent but a small portion of the species there.

Ramsbottom (*Orchid Rev.*, 1922, p. 197), in giving an account of the mycorrhiza of Orchids, says that the fungus in Orchid roots is always the same, viz., *Rhizoctonia* Bern. (*Orchiomyces* Burgeff), except in the case of *Gastrodia elata*, in which the fungus is *Armillaria mellea.* All the normal Orchids' roots have mycorrhiza, except *Wullschlaegelia aphylla*, a saprophyte. This latter case is interesting, as, if some of these saprophytic Orchids do not require mycorrhiza, it might account for the wide distribution of this class of plants, and is of importance, especially in the case of the *Didymoplexis*.

Still, Groom has shown that all the saprophytic Orchids he has examined do contain mycorrhiza in the roots or root hairs.

There is, however, some evidence that Orchid seed can germinate and develop successfully without the aid of mycorrhiza. Prof. Kingdon found nearly 100 per cent. of Orchid seeds germinated on sugar-agar-agar in tubes, and was led to think that the seeds are not so dependent upon certain fungi as upon the nourishment these fungi afford. This has been confirmed by E. Clement, who has shown that many Orchid seeds can germinate in this manner without mycorrhiza, and in the *Orchid Review* and elsewhere he has described and illustrated how he has raised abundance of young plants of *Odontoglossum*, *Miltonia*, *Cattleya* and *Dendrobium* in such manner. *Cattleya* and *Laelia* seed have been successfully germinated on various organic extracts of peat, carrot, etc.

The difficulty of accounting for the occurrence of Orchids in distant oceanic islands is perhaps not so great as at first appears. It seems almost as difficult to account for Orchids occurring on orchard trees or the high branches of forest trees. If an orchard of mangosteen or other trees is planted, and there are Orchids in the neighbourhood, it is only a matter of time before Orchids appear on the branches. Whence comes the mycorrhiza? I have shown in "Symbiosis of Ants and Plants" (*Ann. Bot.*, vol. 24, p. 457) that ants play a great part in supplying Orchids with soil brought up from the ground. It is possible that these insects bring the fungus *Rhizoctonia* with the soil. Ants occur in most tropical islands, and must have arrived with their nests in floating trees or their roots, and might be conveyed to the boughs of trees. Again, the spores of the fungus might be blown across the sea. Though I cannot find that the spore-bearing form of *Rhizoctonia* has been discovered, the wide dispersal of the plant, however, seems to indicate that it does produce spores.

Finally it appears that some Orchids at least can germinate their seeds without mycorrhiza, and although this is done under laboratory conditions, it is possible that similar conditions may occur in oceanic islands.

Distances to which Orchid Seeds are Borne.

The distance to which Orchid seeds can be and are borne by the wind must necessarily be attested by the appearance of plants at some distance from the nearest specimens known, and this is most effectively shown by the

occurrence of species on remote islands, as on the mainland it is not possible to be certain that plants have not occurred at intermediate points between the two localities and to have afterwards disappeared. Even in the case of many remote islands it is not possible to be certain that land did not formerly exist between the two localities, or that neither were larger and projected nearer to each other. Still, on the whole we may be assured that in some cases this never happened, and thus may get some idea of the possible distances to which these very light seeds may be conveyed by the wind. These plants, however, may be transported occasionally by other means less frequently, but this dealt is with later.

The following notes have been accumulated by me showing instances of flight for short distances.

Epipactis latifolia. Terrestrial plant. Mr. Bree (*London Mag. Nat. Hist.*, ii, 1829, 70) says that seedling of this common English plant had appeared at a distance of between 8 and 9 miles from any place known to him where it grew.

Cymbidium Finlaysonianum. Epiphyte, Malayan. In the Singapore Botanic Gardens the seeds flew for a distance of 30 yards and grew on the trunk of an *Arenga* palm. This Orchid was one of the first four species to reach Krakatau after the eruption.

Cymbidium acutum. Epiphyte. The seeds of a plant in the Botanic Gardens flew 60 yards and grew on the trunk of a palm tree.

Agrostophyllum majus. Epiphyte. Capsule small in a dense head of bracts and flowers. Seed flew 90 yards and developed on a palm tree.

Dendrobium pandaneti. Epiphyte. Capsules moderately large, pendulous. Seed flew 1 mile and grew on a tree trunk.

In the case of the last four species the seeds flew from a few feet from the ground where the plants had been planted horizontally, alighting but little higher than the spot from which they started, and I observed that they did not alight on the face of the tree opposite the side they started from, but went round the trunk of the tree and alighted on the further side, so that the seeds of a *Cymbidium* on a tree facing north did not alight on the side of the tree opposite to it, i.e. facing south, but on the north side. There is probably a wind eddy round the trunk which carried the seed round to the back of the tree. I noticed the same phenomenon in *Psilotum complanatum* (*Lycopodiaceae*) in another part of the Botanic Gardens.

The distances recorded above are very short, as some of the seeds found a suitable resting-place on the palms near-by. Most of the seeds were no doubt carried much further, for, as shown in the next section, the seeds can be carried hundreds of miles.

Orchids in Distant Islands.

So far as it is known, no Orchids occur in the following remote islands :—Nova Zembla, Spitzbergen, Ascension, St. Helena, Tristan d'Acunha, Gough Island, Fernando de Noronha, Kerguelen, Amsterdam Isle, St. Paul Isle, Heard Isle, Chagos Islands, Cocos-Keeling, Macquarie, Maldon, Caroline Isles, Marshall Isles, Pitcairn, Easter Isle, Elizabeth Isle, Juan Fernandez and Masafuera, San Ambrosio and San Felix, Maldives, Laccadives, Minikoi, Narcondam.

In some cases the climate and surroundings are perhaps hardly suitable for the plants, and sometimes the nearest coast from which they can come, and from which the wind blows, is poor in Orchids. Both of these factors seem to contribute to the absence of Orchids from Fernando de Noronha, which is only 200 miles from the Brazilian coast, but the nearest land, Rio Grande

del Norte, seems to be very dry, and probably Orchids are scarce there, though they were abundant near Pernambuco. This island bore only one fern (*xerophytic*), very few mosses and hepatics, and no epiphytes, for which apparently the climate was too dry, as epiphytes of all kinds require a fairly moist climate and suffer much from long spells of dry hot weather.

Iceland is 250 miles from the nearest land, Greenland. It contains 13 species of Orchids :—*Orchis maculata*, *O. latifolia*, *O. mascula*, *O. morio*, *O. angustifolia*, *Habenaria viridis*, *H. albida*, *H. hyperborea*, *H. Koenigii*, *Corallorhiza innata*, *Listera ovata*, *Neottia nidus-avis*, *Nigritella angustifolia*.

Azores are nearly 900 miles from Portugal and 550 miles from Madeira. It has 3 Orchids, *Serapias cordigera*, *Habenaria micrantha*, and *H. longibracteata*. The affinity of these plants is with Portugal rather than with Madeira.

Madeira is 450 miles from Morocco. It contains 4 species of Orchids, *Goodyera macrophylla*, *Orchis foliosa* (allied closely to *O. latifolia*), *O. patens* var. *canariensis*, *Habenaria cordata* and *Neotinea intacta*. All are Moroccan or of close affinity to those of Morocco and Southern Europe except *Goodyera macrophylla*, which has no affinity with any plant existing at present in Europe or Africa.

Canary Islands, 50 miles from Cape Juby in Africa. These islands have 6 Orchids, *Orchis patens* var. *canariensis*, *O. longibracteata*, *Ophrys tabanifera*, *Habenaria tridactylites*, *H. cordata*, *Neotinea intacta*. These have affinities or are identical with plants of Morocco and Madeira. The adjacent coast of Africa is desert and quite barren of Orchids.

Cape Verde Isles, 500 miles from Africa, 1 Orchid, *Habenaria petro-medusae*, probably derived from some African plant.

Bermuda, 580 miles from North Carolina. It has only 1 Orchid, *Spiranthes tortilis* of North America. The adjacent coast is poor in Orchids.

South Trinidad, 600 miles from South America. It contains at least 1 Orchid. Nichol (in "Three Voyages of a Naturalist," p. 56) writes : "On the trunk of one of the tree-ferns Mr. Meade-Waldo found one "Orchid, which he sent home to England." I have no record of the genus of the plant, but it was apparently an epiphyte.

Socotra, 500 miles from Cape Guardafui, Africa. It has 1 species of *Habenaria*, an endemic one. The nearest land is very poor in Orchids.

Aldabra, 220 miles from Madagascar, has 3 species, all epiphytic, 1 *Acampe* (allied to a Madagascar species) and 2 *Angraecum*. (1 *A. eburneum* also is found in the Seychelles.)

Seychelles, 900 miles from Mauritius, has 10 species of Orchids, *Liparis*, *Microstylis*, *Phaius* and *Calanthe* (terrestrial), and *Bulbophyllum*, *Angraecum* and *Agrostophyllum* (epiphytic).

Agalega Island, about 400 miles from Madagascar, has *Disa tripetaloides* (terrestrial).

Many of the small islands in the Mascarene group possess no Orchids. The flora of the bigger islands, Rodriguez, Bourbon, etc., is allied to that of Madagascar, and it seems probable that they were all much larger at one time and more closely connected, forming continental islands.

The Andaman Islands, 320 miles from Tenasserim. They contain a considerable number of Orchids, all of Tenasserim affinity, some endemic species, but many identical with those of Tenasserim and Burma, such plants as *Microstylis congesta* and *Eulophia graminea* (terrestrial), and *Dendrobium crumenatum*, *D. secundum*, *D. grande*, *Bulbophyllum clandestinum*, *Pholidota imbricata*, *Vanda teres*, *Cymbidium aloifolium*, most of which are also common over the whole Malay region.

Barren Island, 60 miles from the Andamans, has *Dendrobium* species and *Pholidota imbricata*.

The Nicobars, 80 miles south of the Andamans and 110 miles from Sumatra. 4 epiphytic Orchids are known from them, *Dendrobium anceps*, *Vanda teres*, *Phalaenopsis cornucervi* and *Saccolabium obliquum*. The flora, however, has not been thoroughly explored.

These islands are also a continental group, and were probably formerly connected with the mainland of Tenasserim.

Christmas Island, 194 miles from Java, contains 10 species of Orchids, *Dendrobium crumenatum*, *Desmotrichum pectinatum*, *Phreatia Listeri* and *Ph, angusta*, *Saccolabium Archytas*, *Dendrocolla carinatifolia*, *Thelasis elongata*, (all epiphytic), *Corymbis angusta*, *Didymoplexis pallens*, *Zeuxine exilis* (terrestrial). All are of Malayan type and identical with or closely allied to Javanese species, except the *Dendrocolla*, which occurs in the island Pulau Aur, off the Malay Peninsula coast.

Krakatau.—The Orchids which appeared here after the eruption, which destroyed all the vegetation, were *Cymbidium Finlaysonianum*, *Vanda Sulingi*, *Liparis viridiflora*, *Oberonia* species, *Thrixspermum* species (epiphytes), *Arundina speciosa*, *Phaius* species, *Spathoglottis plicata*, *Eulophia macrostachya*, *Habenaria* species, *Peristylus* species, *Nervilia aragoana* (terrestrial).

The first to arrive were *Arundina*, *Phaius* and *Spathoglottis*, and *Vanda Sulingi*, fourteen years after the destruction of the former vegetation. It must be remembered that Orchids usually take a number of years to grow before they are identifiable. They were preceded by some ferns and a few (mostly seashore) flowering plants only.

Norfolk Island, 400 miles from New Zealand and the same distance from New Caledonia. Of its 7 Orchids, 6 are Malayan types and 1 New Zealand. *Oberonia* (2 species), *Dendrobium* (2 species), *Bulbophyllum* (1 species), *Phreatia* (1 species), epiphytic and Malayan; *Microtis porrifolia* (terrestrial), New Zealand.

Kermadec Isle, 700 miles from New Zealand, has 2 New Zealand terrestrial plants, *Microtis porrifolia* and *Acianthus Sinclairi*.

Chatham Island, 360 miles from New Zealand, has 9 Orchids, all New Zealand plants or with that affinity, *Acianthus*, *Corysanthes*, *Microtis porrifolia*, *Pterostylis* (3 species), *Galeola*, *Caladenia*, *Chiloglottis* (terrestrial), *Earine* and *Sarcochilus adversus* (epiphytes).

Auckland Isles, 180 miles from New Zealand, have 8 terrestrial Orchids, *Thelymitra*, *Lyperanthus* (1 species each), *Caladenia*, *Chiloglottis*, *Corysanthes* (2 species each):

Campbell Island.—Has 2 species (both New Zealand).

The last four islands were probably connected by land at one time with New Zealand, and the Orchids are all New Zealand types. It is remarkable that in Norfolk Island the Orchid flora is almost entirely Malayan.

Falkland Isles, 300 miles from Patagonia, have 4 terrestrial Orchids, *Chloraea* (1 species), *Asarca* (2 species), *Codonorchis* (1 species).

All of these are either Patagonian or allied to Patagonian species.

Tahiti.—Contains 33 species, 16 terrestrial—*Microstylis*, *Liparis* (4 species), *Spathoglottis*, *Calanthe*, *Arundina*, *Hetaeria*, *Moerenhoutia*, *Nervilia*, *Habenaria* (2 species); epiphytes 17, *Oberonia* (2 species), *Dendrobium* (4 species), *Bulbophyllum* (2 species), *Eria*, *Phreatia* (3 species), *Earine*, *Taeniophyllum* (4 species). All are of Malayan affinities except *Earine*, which occurs in New Zealand, but it seems more probable that it originated in Polynesia and spread thence to New Zealand.

Sandwich Islands.—These are 2,350 miles from South America and 700 miles from the nearest Polynesian Islands, which, however, do not contain any Orchids so far as is known, but it is probable that great changes in land surface have taken place here, and Orchid-bearing areas may have been more extensive at one time. There are only 3 species, a *Liparis*, an *Anaectochilus* and a *Habenaria*, all endemic and terrestrial, and all of Malayan affinity.

Galapagos Islands, 600 miles from South America. They contain 5 species of Orchids, all American or of American affinity. *Epidendrum* (2 species), *Ionopsis utricularioides*, *Ponthieva maculata*, all epiphytic, and a *Govenia* or *Eulophia*, terrestrial.

There is some reason to believe that these islands were at one time attached to the mainland.

In these islands the genera which occur most frequently are the following :—

Habenaria.—Iceland, Canaries, Madeira, Azores, Cape Verde, Socotra, Andamans, Tahiti, Sandwich, Krakatau.

Liparis.—Seychelles, Tahiti, Sandwich, Krakatau.

Calanthe and *Bulbophyllum.*—Seychelles, Tahiti, Norfolk Island, Krakatau.

Phreatia.—Christmas Island, Norfolk Isle, Tahiti.

Dendrobium.—Andamans, Nicobars, Christmas Island, Norfolk Island, Krakatau.

All of these genera, except the last two, occur all over the tropics of both worlds. *Habenaria* in the large sense is found equally in temperate regions, even the arctic zone, and it is also abundant in the tropics. The species are low-growing herbs found usually in open country and even deserts, and less frequently in forests.

Phreatia is interesting, as the species are small epiphytes with tiny flowers and fruits in short spikes.

Goodyera macrophylla of Madeira is a very remarkable plant. It is endemic and has no affinity with *G. repens*, the only European species, and no species of the genus has been found in Africa. It does not belong to the same section of the genus as *G. repens*, but to the section *Georchis*, which might be generically separated and is characteristic of tropical Asia.

From the study of the insular Orchids we see :—

(1) That the nearer the island is to an Orchid-bearing region, continent or continental island, provided that Orchids are abundant there, the larger is the number of species.

(2) That the number of species depends on the abundance of plants of the order on the nearest land, but that in islands unsuited by dryness or other such circumstances, even if near a country well provided, such plants may be quite absent, as in Fernando de Noronha and Cocos-Keeling Islands.

(3) That in islands, especially the remote ones, there is usually 1 (rarely 2 or more) species representing each genus. This is, however, very characteristic of all plants in oceanic islands.

(4) That the distances to which Orchids can migrate across the sea by wind are very great. Indeed (except ferns and other cryptogams), they seem to be able to go further than any other wind-dispersed plants, although plumose fruits and seeds are nearly as successful in establishing themselves on islands.

The longest distances recorded of Orchids traversing the seas are 900 miles to the Azores, 700 miles to Sandwich Isles, 600 miles to Galapagos, South Trinidad and Kermadec.

(5) That taking only the tropical and sub-tropical area where epiphytes can grow, the low-growing terrestrial kinds can travel at least as far as the epiphytic Orchids, although the latter, from their higher and more exposed position, would seem to have the better chance of sea-traversing.

Other Methods of Dispersal of Orchids.

Although the dispersal of Orchids is usually by the flight of their very light seeds in the wind, there are a few other factors which must be taken into account. *Vanillas* possess banana-like baccate fruit with small round seeds, and are dispersed by birds or mammals.

Mr. Woodruffe-Peacock gives an instance of the seeds of the Tway-blade (*Listera ovata*) being borne to a distance by attachment to human clothes.

Mr. Guppy suggests that the seeds of the Sandwich Island Orchids might have been transported to these islands by attachment to insects. Though it is possible, there is no evidence of this ever having occurred, and there is no need to account for the Orchids having reached this spot in this way, as the distance is not greater than that between other islands and the mainland, and the seeds could quite well travel by air. It would be equally possible for the seeds, especially of epiphytics, to travel on the feathers of birds.

Occasionally undoubtedly pseudobulbous Orchids travel by sea as live plants. I have mentioned elsewhere that I have seen quite fresh plants of *Dendrobium crumenatum* floating in the sea, and Moseley ("Notes of a Naturalist," p. 316) states that he found on the beach of Little Ki Island a large mass of pseudobulbs of an epiphytic Orchid with roots complete, cast up by the sea, buried at the foot of a tree, and quite lively.

As a rule, however, Orchids are very sensitive to the action of sea-water, and usually perish very soon, although there are a few which apparently live habitually on seashore rocks where they must often receive the splash of the sea. Terrestrial Orchids, however, and non-pseudobulbous kinds, could hardly survive immersion in salt water.

SPOROPHYTES.

Filices (Ferns).

The distribution of ferns over the world is very extensive. They are practically excluded only from deserts or very dry spots, and from the coldest parts of the Arctic and Antarctic regions. Though most abundant in both number of plants and species in the hot, wet tropical forests, they extend to and are well represented in the temperate regions and in most of the oceanic islands where the climate and soil are suited to their development. Of vascular plants they are the first to arrive on any new and suitable ground. Thus in Krakatau in 1886, when the island was first examined by botanists after the destruction of the flora three years before, 12 species of ferns were found as against 3 wind-dispersed *Compositae* and grasses and 9 sea-borne other plants.

Their absence from most coral atolls is to be attributed to unsuitable environment. On old walls, tree trunks, and such suitable positions in warm wet places, the advent of the flora is the same as in Krakatau. First appear the soil bacteria and the blue-green algae, then the mosses. These make the first soils, on which then appear the ferns, followed by the flowering plants.

The appearance of ferns in what may be called new ground of course depends largely on the suitability of spots for the evolution of the prothalli

into adult plants. In the volcano crater of Papandayan, in Java, the plants which went furthest towards the centre, and throve regardless of the sulphurous smoke pouring out from the fumaroles, were an aquatic alga and the stiff-fronded xerophytic fern *Phymatodes platyphylla*, and the last plant to be met with on ascending the barren, broken rocks of the volcano Sibayak, in Sumatra, was the fern *Litobrochia incisa* in low dense masses. No flowering plants were to be seen for a considerable distance from either of these ferns. This was obviously because seeds of flowering plants which were able to reach these spots failed to grow in these localities.

Many years ago I introduced the Hart's Tongue fern (*Scolopendrium vulgare*) into our garden in Cobham, Kent. This fern did not grow anywhere in this region in a wild state. In a very short time it spread from the fernery to the damp sunk entrance of a cellar, and flourished in abundance, and also to the outer side of the wall facing the village street, where a number of plants appeared. They spread no further, however, and not long after disappeared, having failed to establish themselves. Why some ferns seem able to grow in unexpected spots and others do not, and why they utterly fail to establish themselves in localities where they might be expected to do so, is still quite obscure.

It is quite clear, however, that the abundance of an early evolved group of plants like the ferns is not at all due to the great age of the order. The *Lycopodiaceae* and *Equisetaceae* are ancient orders, and the *Cycadaceae*, geologically speaking, are also of great antiquity, but of these none are now as widely spread or as abundant as ferns.

The earliest forms of ferns have long disappeared, and if some genera, e.g., *Matonia*, *Marattiaceae*, and other forms of considerable age, are still represented in the world, they have become very local and are confined to a few spots. Their wide distribution is due to their extremely light spores being easily borne all over the world by wind, and their adaptability to develop and reproduce themselves in a variety of localities, climates and environment. The dispersal of ferns is almost entirely due to wind. There are a few cases in which the distribution of species is due to human agency to some extent, e.g., *Pteris aquilina* (*see* that section), some species of Maidenhair ferns, *Adiantum* and *Cheilanthes farinosa*, garden escapes, but otherwise there seems to be no method by which ferns are dispersed except by the action of wind, and in this way they resemble the equally widely distributed *Orchidaceae*, which, however, are not by any means so abundant as ferns, for the reason that their requirements as to environment, insect fertilisation, etc., are more exacting.

Guppy ("Notes of a Naturalist," p. 230) writes of the Hawaiian and Tahitian floras :—

"The agency of the winds in dispersing the spores of Ferns and Lycopods "has been relatively uniform through the ages when compared with the varying "agency of the migrant bird, to which the flowering plants mainly owe their "distribution. Thus it is that in the Pacific islands the vascular cryptogams "have experienced less differentiation than the flowering plants, though, as "a rule, far older denizens of the islands. Yet we cannot doubt that the same "principle has been at work in both cases, the difference arising in the instance "of the flowering plants from the interrupted and often suspended agency "of birds in the work of dispersal."

He suggests also that these light spores of ferns and *Lycopodiaceae* may have been transported from place to place by insects, but though undoubtedly possible, we have no evidence of this.

Of ferns we have all sizes, from the small *Trichomanes parvulum*, 1½ inches tall, and *T. motleyi*, even smaller, to the big *Angiopteris*, with fronds up to

10 feet long, and Tree-ferns, *Alsophila*, etc., 30 or more feet tall; but though the spores are more abundant and more exposed to the wind in these taller plants than in the little *Trichomanes*, hidden away on the lower branches and stems of the trees of the dense dark forests, there is no apparent difference in the wideness of the area they cover. *Trichomanes parvulum* ranges from the Mascarene Islands to Southern India, Java, Christmas Island, China, Japan, to Polynesia, and *Angiopteris* from Madagascar through Indo-Malaya to Australia. However, the open-country *Ophioglossum*, *Helminthostachys*, *Osmunda*, have the sporanges borne on tall or at least elongated spikes above the grasses and moorland vegetation among which they largely grow.

Prof. F. O. Bower (in "Ferns," vols. i and ii) gives the number of spores produced by various ferns in the sporanges in the sorus, so that we are able to get at the number of spores produced by a frond and by the whole plant in, say, a year. It will be seen that the number of spores produced varies very greatly.

	Number of Spores in a Sporange.	Number of Sporanges in Sorus.
Ophioglossum pendulum	15,000	
Botrychium lunaria	2,000	
Christensenia	7,850	
Marattia	2,500	12
Angiopteris	1,450	8–15
Gleichenia flabellata	512–1,024	
Gleichenia, other species	256	
Hymenophyllum tunbridgense	420	20
" *dilatatum*	128	90
Trichomanes radicans	64	140
" *reniforme*	256	40
Platycerium	64	
Cheilanthes	32	
Ceratopteris	10–32	

I have taken only a selection from the large numbers of figures given.

Prof. Bower gives the output of spores per sorus as follows :—

Marattia fraxinea	45,000
Polypodium aureum	57,000
Angiopteris evecta	14,500
Alsophila excelsa	3,250
Gleichenia flabellata	3,000
Hymenophyllum tunbridgense	8,400
" *dilatatum*	11,500
Trichomanes reniforme	10,240
" *radicans*	8,960

It is clear that the area of dispersal covered by a fern bears little or no relation to the output of spores by the plant, for it may be noticed that *Hymenophyllum tunbridgense* has fewer spores to a sporange than *H. dilatatum*, and *Trichomanes radicans* fewer than in *T. reniforme*, yet the first of each pair mentioned is much the widest dispersed of the two plants, both being widely scattered all over the world, while the other two are very local. I take six of these ferns for comparison :—

Marattia fraxinea.—A plant with a round fleshy base bearing about 6 fronds of large size. These plants have 14 pinnas bearing 41 pinnules, each of which

has 200 sori. Bower gives the spores as 45,000 to a sorus, so that this plant produces 30,996 millions to a plant.

Angiopteris evecta.—A similar plant with 4 fronds, each bearing 14 pinnas and 20 pinnules to a pinna, sori 200 to a pinna and 14,500 spores to a sorus, giving 32,480 millions to a plant.

Hymenophyllum tunbridgense.—A dwarf plant with slender rhizomes forming a mass or tuft of very numerous fronds. Each frond has 5 to 8 sori containing 8,400 spores, or 67,200 to a frond.

Hyemenophyllum dilatatum.—Has more distant fronds, with 110 sori on each. Spores, 11,500 in a sorus. Total for a frond 1,265,000.

Trichomanes reniforme.—Fronds solitary, distant on a slender rhizome, with from 55 to 142 sori. Spores in a sorus 10,240. Taking an average of 100 sori to a frond, total spores 1,024,000.

Trichomanes radicans.—Is a tufted plant with about 8 fronds in a tuft, each bearing 300 to 400 sori. Taking 400 as typical, this gives 3,584,000 spores on a frond and 28,672,000 to a plant.

Here *Marattia fraxinea*, with 30,996 million spores to a plant, is more widely distributed than *Angiopteris evecta*, with 3,248 million, the former occurring in the tropics of both worlds, while the latter, which is actually a commoner plant in its area, is confined to tropical Asia, Madagascar, Australia and Polynesia.

Hymenophyllum tunbridgense, distributed over the world, has 67,200 spores to a frond, while *H. dilatatum*, confined to Malaya, Australia, New Zealand and Polynesia, has 126,500 to a frond.

Trichomanes reniforme, of New Zealand and Australia, has 1,024,000 to a frond, and the world-wide *T. radicans* 3,584,000.

The number of spores discharged by ferns is thus seen to be enormous, and bears little relation to the wide area occupied by the species, or the number of plants in the world, for in many cases of rare species the spores produced in one season must be much in excess of the number of plants in the world.

It may be taken, as a rule, that in ferns the first comers to a new island are the terrestrial ones, as the epiphytes require a growth of arboreous vegetation before they can establish themselves. Thus in Krakatau the first 12 species were all terrestrial, and one more, *Drynaria quercifolia*, appeared a few years later. By 1919 43 species had settled in the island, of which altogether 14 were epiphytic.

Many of the commonest and most widely distributed of the species in the area nearest to the islands are among the first to arrive, or may be the only species there, such plants as *Thamnopteris nidus*, *Pleopeltis phymatodes*, *Nephrodium molle*, and the various species of *Nephrolepis*.

This seems certainly due to the adaptability of the commoner forms to varied environment, and to the extent of habitats similar to those on which they grow on the nearest mainland.

In Christmas Island *Nephrolepis exaltata* and *N. acuta*, which grow in open woods and cleared ground in the non-calcareous country of the Malay Peninsula, grow on the raised coral reefs of the island, being an illustration of remarkable adaptability. *Nephrodium truncatum*, on the other hand, was quite confined to spots where the basalt rising to the surface of the ground permitted the fresh water to come up as a spring. It was evidently a plant which could not grow on the dry calcareous coral reefs. The spores of this, and probably many other ferns, must have been borne by the wind from Java and fallen on the island in abundance, but only those which fell on the freshwater spring ever developed into adult ferns. *Acrostichum aureum*, a tidal mud fern, occurs in practically all tropical mud-banked tidal rivers, and though adult plants will continue to live for very many years inland, long after the tidal creek in which they grew at first has been silted up, so that they are now far

away from brackish or salt waters—as I have seen them in Singapore Botanic Gardens and in the interior of forests in Johor—their spores are probably all wasted, never reaching to any position in which they can develop.

It will be seen from the dispersal of ferns to oceanic islands that, as in flowering plants, an area is invaded by ferns from the nearest available land producing them. Thus the ferns which first invaded Krakatau were Javanese species, as were those inhabiting Christmas Island. In the Azores, species from Western Europe and Madeira are found; in Juan Fernandez, those of Chili; in St. Helena, some from South Africa, others from Tristan d'Acunha.

A few species of ferns have a curiously sporadic distribution which is difficult to account for unless they have disappeared from some cause in intermediate stations, such plants as *Asplenium monanthemum*, which is found only in Africa, Madeira, Azores, South America and Polynesia, and one locality in the Eastern Malay Peninsula.

There are few islands, however distant from the mainland or larger islands producing ferns, where these plants are not to be found, and these are chiefly coral atolls, where the environment is unsuitable.

Some notes on far dispersal of ferns and other sporophytes are given here to show the immense distances that spores can go, though much more research is wanted in the case of *Mosses* and *Hepatics*.

The Hawaian Islands are 2,350 miles from the South American islands. The South American ferns in Hawaii are *Schizaea robusta*, *Asplenium fragile* from the Andes, *A. aspidioides* from the Andes (also found in Africa and India), *A. monanthemum* from the Andes. There seems to be no evidence that Hawaii was ever connected with South America by land, and this is endorsed by the flowering plants, with the exception of some sea-dispersed species, being all of Polynesian affinities. Nor is there any reason to believe there were any islands at any time between the two localities on which these fern spores could have rested and carried on the migration. So that if we allow that the spores of these American ferns were carried by wind to the Hawaiian Islands, this gives a much wider range of flight to fern spores than is possessed by Orchids or any other wind-dispersed plants. The *Selaginellas* of Hawaii have all Polynesian affinities.

In Ascension Island we find that the bulk of the sporophytes, Ferns, Mosses, Hepatics, etc., are of St. Helena type and affinities. St. Helena has rather a curious mixture. The majority of the ferns come from South Africa and the Mascarene Islands (1,140 miles), some come from Tristan d'Acunha, and some from the northern region, Cape Verde and such spots. Some of the mosses are South American (1,800 miles away). In Tristan d'Acunha most of the ferns are natives of South America, 5,520 miles away; *Nephrodium tomentosum* and some of the mosses are Mascarene.

The sporophytes of Marion Island are chiefly Antarctic South American, about 1,500 miles away. Amsterdam Island has *Gleichenia polypodioides*, only known from South Africa, and *Monogramme graminea*, also South African and of Tristan d'Acunha.

All the Azores ferns and mosses are apparently derived from the Canaries and Madeira or Southern Europe, except *Lycopodium cernuum*, possibly from Africa, and *Selaginella Kraussiana* from Madeira and South Africa; but I am doubtful about the latter, for it is a plant commonly cultivated in gardens, and if not actually introduced into the Azores by man, may have been introduced into Madeira and thence spread to the Azores by wind. The distance of the Azores from Madeira is 550 miles.

These notes show the great distance of spore-travel, and we can hardly wonder at the wide distribution of such plants as *Pteris aquilina*, *Hymenophyllum tunbridgense* and *Trichomanes radicans*. The limited distribution of

many species, however, is equally striking. Abundantly as spores are produced, one rather wonders at the absence, say, of the bracken from so many spots. Why did it not reach the Pahang plateau till accidentally brought by man, abundant as it is some few miles away? Here, however, the question of *limit* and the causes of limit comes in, and of these we as yet know little.

Mr. C. E. Benham (in the *Journal of Botany*, 1924, p. 146, and 1925, p. 213) describes and comments on the appearance of ferns under bottles sunk in the ground. It had been noticed that in almost every case where wine bottles had been sunk mouth downwards in the ground, one or more ferns had appeared. In one case a spleenwort (*Asplenium*) had appeared in this way, though none had been in the garden for twenty years, and previously the ground had been a potato field. Further examination proved that the fern spores were in the top layer only of the soil, and were mainly found in spots, especially at the foot of walls, favourable to wind-drift from the south-west. The plants were obtained by placing soil in water, where it sank, leaving as a scum the light material which contained the spores, and this was sown on sterilised soil. Now, in most cases at least, the spores must have come from a long distance and must have fallen in immense abundance. In fact, the continuous rain of fern spores must resemble that of the terrestrial algae and fungi. Fern spores, as is shown, can travel for hundreds of miles by wind, and many species are very widely diffused, so that it is rather remarkable that many are so local in their habitats, and that species are not more abundant in Europe. Many species are cultivated in gardens, and in towns one often finds seedlings, which have obviously escaped from gardens, growing on the walls of the streets, at least for a time, but I do not know of any species which has established itself in Europe as a " garden escape." The puzzle is not so much why ferns are widely dispersed and abundant in some places as why there are not more of them.

LYCOPODIACEAE.

Of these, *Lycopodium*, *Psilotum* and *Selaginella* are wind-dispersed, as the spores are as light as those of ferns. They are, however, very much less abundant, probably on account of their rather special requirements as to environment. The *Lycopodiums* are either terrestrial, open-country plants or (in the tropical rain-forests) epiphytes. *Psilotum* is a tropical or sub-tropical epiphyte which occasionally grows on old walls in the tropics. *Selaginella* is found in greatest abundance in dense tropical forests, a few in open country, mountains and even deserts. The area occupied by the epiphytic *Lycopodiums* and *Psilotum* (2 species), is limited to the area in which epiphytes can grow successfully, which is practically only the warm wet regions of tropical Asia, Africa and South America. The terrestrial *Lycopodiums* are more abundant in the temperate regions, but two or three are found in hot regions, usually in open places or along river banks.

The *Lycopodiaceae* are, like the ferns, dispersed mainly by their wind-borne spores, though some are also dispersed by bulbils. Bulbils occur on not a few ferns, but, so far as it is recorded, they are not wind-dispersed, but merely fall to the ground and continue their growth. Of *Lycopodiaceae*, Kerner (Nat. Hist. Plants, ii, p. 817) writes :—

" Bud-shaped offshoots which become detached from aerial portions of " plants, and whose distribution is effected by wind, are comparatively rare. " A remarkable instance is furnished by the Club moss (*Lycopodium selago*). " This plant, which is found in mountainous districts in the Northern " Hemisphere of the Old and New Worlds, forms buds in the axils of its stiff, " dark green leaves, especially near the top of the shoot, which might at

"first sight be taken for small winged fruits. These buds are so provided with "little leaves as to offer a good purchase to the wind, and by this means they "are transported. The North American *L. lucidulum*, *L. reflexum*, *L. serratum*, "*L. erubescens*, behave in just the same way as *L. selago*."

The most widely dispersed and abundant *Lycopodium* is *L. cernuum*, a tall terrestrial species usually about a foot or two high, but scrambling sometimes up to 20 feet, with numerous small, pendent cones of sporanges. It grows in open dry spots, heaths and borders of woods, often in great abundance. It is absent from dense forests, but when roads are cut it often follows up along them, though it becomes thin and weak in shade. It is abundant in India, Ceylon, the Malay Peninsula and islands, and Polynesia, occurring in most of the islands, North Australia and New Zealand, China, Japan, and tropical Africa and America. Of outlying islands it is found in the Azores adjacent to hot springs, and solfataras, Ascension, St. Helena, St. Paul's Island (also near hot springs), Kermadec, Formosa, Hainan, Mascarene Islands, Krakatau, Narcondam. In fact, it seems to be diffused over all countries where it is warm and damp enough for it, and to colder places by volcanic springs. The other terrestrial *Lycopodiums* are in some cases widely spread; those of the temperate mountain regions, *L. selago*, *L. complanatum*, are widely scattered over the mountain-sides and moorlands of the temperate regions.

L. selago, common in Europe, north temperate Asia, North and South America, and Hawaii, is also found in Madeira and the Azores. *L. complanatum* also occurs in Madeira and the Azores, the north temperate region, Indo-Malaya, Madagascar and tropical America.

L. saururus, a terrestrial species resembling *L. selago*, is found in the Argentine Andes, the Cameroons, and Mascarene Islands, Juan Fernandez, St. Helena, Tristan d'Acunha, Marion Island and Kerguelen. Some of these island forms have been made into distinct species by botanists, but there can be little doubt but that they are local strains. The plant is so closely allied to *L. selago* that it has been sometimes referred to it. It appears to take the place of *L. selago* in the southern hemisphere.

The epiphytic species of *Lycopodium* are much less widely distributed than the terrestrial. They are abundant in the tropical rain-forests of Asia, but, except in South Africa and Madagascar, they are almost entirely absent from Africa, one species being reported in the Cameroons. It is suggested that these plants are parasitic on certain trees, but this is doubtful. *L. squarrosum* reached Krakatau by 1919, and *L. phlegmaria* I found plentiful in Christmas Island. Both are common on various trees in the Malay forests, but all species of epiphytic *Lycopodium* are practically impossible to maintain in cultivation. They seem to have certain requirements which are obscure, and which we cannot or do not give them in cultivation. Probably these unsatisfied demands restrict their spread.

The same wide distribution is seen in *Psilotum*, which seems, in many parts of the Malay Peninsula at least, to produce itself by bulbils. It is, however, more widely dispersed by the spores. There are two species occupying much the same area, but *P. triquetrum* is by far the most common. It is abundant in India, the Malay Peninsula and islands, South China, Japan and Polynesia (apparently absent from Africa except Natal and Mozambique), Mascarene Islands and South America, and the West Indies. It is very much of an island plant, occurring in such distant isles as Norfolk Isle, Kermadec, Pitcairn, Dane's Island (12 miles distant from Canton), Formosa, Hainan, Chagos (Diego Garcia), Ascension, Bermudas, Galapagos, Maldives, Minikoi, Krakatau (1919), Narcondam. The plant grows on trees as an epiphyte, also on rocks, especially volcanic lavas, and on ruined walls.

P. complanatum grows frequently on mangrove trees, and is less abundant. It occurs in the Malay Peninsula and islands, Polynesia, Australia, Seychelles, Mexico and the West Indies. The spores of *Psilotum* are evidently very widely dispersed by the wind.

SELAGINELLACEAE.

The *Selaginellas* are less widely dispersed than ferns. They are low-growing terrestrial plants, usually found in dense forests, produce comparatively few spores, and are mainly tropical. A few are found in temperate and cold climates, and some in dry desert regions, where they are dispersed as tumble weeds (*see* p. 35). They are very scarce in oceanic islands. In Krakatau *Selaginella plana* appeared in 1919. In Christmas Island an endemic species, very scarce, *S. rupestris*, was obtained. *S. Kraussiana* occurs in Madeira, the Canaries and Azores, and is widely scattered over Africa. *S. Azorica*, an endemic species, also occurs in the Azores. This gives a distance of at least 550 miles for the flight of the spores, but, as is elsewhere suggested, *S. Kraussiana* is cultivated as a garden plant and may have run wild.

EQUISETACEAE.

The genus *Equisetum*, all that now remains of this early order, is much less widely dispersed and abundant than either ferns or Lycopods. They chiefly inhabit temperate regions, but a few find their way into the tropics.

As inhabitants of distant islands they are scarce, chiefly from the fact that the oceanic islands are not well provided with localities sufficiently wet and suitable for their habitat.

Equisetum ramosissimum occurs in the Canaries. It is a native of Morocco and Southern Europe, Asia Minor, India, China, Formosa, Borneo, South America, and South Africa. *E. Telmateia*, a native of Europe, Algiers, India and North America, is also found in Madeira. *E. debile*, a native of all warm Asia and Africa and Polynesia, reached Krakatau by 1919. *Equisetum pallidum* occurs in the Cape Verde Isles. The spores are borne on tall spikes and apparently diffuse freely.

MUSCI (MOSSES).

Mosses are abundant all over the world wherever it is damp enough for them to grow. They are dispersed by the aid of their minute spores, and also to a considerable extent locally by bulbils or small detached portions of the plant, which can be blown along by the wind.

They are among the first plants to appear on new ground in suitable localities where they can grow, and some have been found in nearly all the oceanic islands in which they have been sought for. However, the ordinary, and especially the early, botanists have very frequently neglected to search for these and the more primitive cryptogams. They are certainly very scarce in dry localities, both desert areas and xerophytic islands. Only one species, *Bryum rufescens*, is recorded for Cocos-Keeling Island, and I found only 5 species in Fernando de Noronha, and those were few in individuals. The distribution of mosses is comparatively little known, as the ordinary plant-collector seldom troubles to collect them. Only two were recorded from Krakatau, which were collected three years after the catastrophe; but Max Fleischer (*Ann. Bot. Gard*, xxxii, 105) gives a list of 19 species obtained in 1922, all Javanese species, one, however, mainly known from south-east Sumatra.

Dispersal of Bulbils or Thallidia.—Many mosses, as well as hepatics,

produce very small bulbils or thallidia, which are distributed by wind or water. In *Syrrhopodon scaber*, of South America, these are borne on the tops of leaves. *Tetraphis pellucida* bears at the top of special shoots disc-shaped bulbils supported on delicate filamentous stalks and embedded in a cup of crowded leaves. The fine stalks wither and the bulbils are whirled away by the wind. In many other mosses small shoots are detached and blown away by wind, to take root and grow elsewhere (Kerner). The Rev. H. H. Higgins, the author of "Notes by a Field Naturalist in the Western Tropics," mentions "a moss "resembling some British species of *Campylopus* in Dominica (*Neckera tricho-"phylla*) in which the leaves were rigid and bristle-pointed, with very short fronds "shaped like a closed parasol, and most of the stems of which ended in long "plumes. On examining this moss (dried) it was found that the tufts had broken "up into single stems and then had travelled in all directions through the dried "moss." Many mosses with rigid bristle-pointed leaves are in the habit of shedding single stems, which lie scattered on the surface of the tuft till the wind wafts them away, and when they fall among dried stumps of grass they are able to travel till they reach a suitable resting-place. Some of these, e.g., some species of *Campylopus*, rarely produce capsules; others bear capsules on a curved footstalk, so that the spore-case sheds the spores on the plant itself, which, being capable of motion, bears away the spores to a suitable spot.

A very valuable and interesting study of the dispersal of the spores of mosses is given by Captain F. W. Hutton in "Observations on the Different Modifications of the Capsule of Mosses" (Trans. New Zealand Inst., vii, 342). He remarks :—

"It is evident that if the spores were to be blown away by the first puff of "wind that occurred after they were ripe, or to be all knocked out by a drop of "rain that fell on the capsule, they would have little chance of being dispersed "widely. If also the spores escaped in wet weather they could not travel far, "for they would stick to the first leaf or stone they were blown against. It "is necessary, therefore, that to be widely dispersed they should be held fast "in wet weather and let loose in dry, in order that some might be driven off in "one direction, some in another, so as to be scattered as far and as wide as "possible."

As they inhabit very different stations, e.g., among long grass, on exposed walls, on trees and under water, in sheltered ditches and on mountain peaks, different combinations will be required by different species. Species which grow in long grass require a long fruit-stalk to elevate the capsule above the grass and so let it be exposed to wind, while this would be detrimental to the mosses which live in unexposed situations, and which generally have the fruit-stalk so reduced that the capsule is buried and protected by the perichaetial leaves. In order to obviate the danger of the spores being released during wet weather, when the wind could not disperse them, there are a variety of modifications in the capsule so as to retain the spores till the air becomes sufficiently dry, recalling the modifications or adaptations in many of the capsular herbs such as *Silene*, *Linaria* and *Antirrhinum*, though the reason for the adaptation of the capsule in these cases is somewhat different.

In the lowest forms of mosses, *Phascei*, the capsule, which is rounded, simply decays and dehisces irregularly, so that the spores are quite exposed to the elements, except in species in which the capsule is sunk among the perichaetial leaves. In *Phascum cuspidatum* the leaves open when wet and close over when dry, and thereby protect the spores to some extent. The spores are few in these mosses: *P. alternifolium* has about 16 in a capsule, and *P. serratum* has about 100. These plants inhabit ditches, banks and other sheltered situations.

In the *Andreaceae* the ellipsoid capsule splits longitudinally into 4 or

more segments, which remain joined at the tip, so that the spores escape through the lateral slits. The valves bend outwards when dry, so as to open the slits, but when wet straighten up and close the capsule. They grow on exposed mountain rocks.

In mosses in which the urn-shaped sporange or capsule is covered with an operculum, the operculum simply falls off when the spores are ripe. In *Braunia, Phycomitrium* and *Aulacopilum* there is nothing to prevent the spores being blown out at once, but *Helwingia* and *Leptangium* have the capsule immersed in the leaves, and so is partly protected. In *Sphagnum* the globose capsule has the operculum and spores blown out to a distance of 6 or 7 inches by the compressed air which has penetrated into the capsule through the stomata.

The next stage of evolution is the development of a flexible ring of very hygroscopic cells called the Annulus, between the mouth of the capsule and the operculum, which protects the spores to some extent from the wind (*Anoectangium* and *Calomnion*). In some *Gymnostomum* and some *Calomnion* the wall of the capsule is thickened at the mouth so as to reduce the size of the opening. In most genera in which the apparatus for protecting the spores is more perfect, the annulus falls off when the operculum is detached, but in the above-mentioned genera it persists. In *Anoectangium* the spores are very minute and numerous, but Hutton could not trace any connection between the size of the spores and the abundance or rarity of the species.

A large number of mosses possess a series of teeth round the mouth of the capsule, the "peristome." In the most complete state the peristome has 16 teeth, sometimes split half-way down (*Dicranum, Fissidens*), and sometimes divided to the base, making 32 (*Trichostomum, Tortula*), while sometimes 2 teeth are joined together, making 8 (*Octoblepharum*), and sometimes reduced to 4 (*Tetraphis*). Inside the outer peristome is often found an inner one. In some species (*Weissia, Didymodon, Conomitrium*) the teeth are short and fragile, and soon break off, but in most genera they are strong enough to prevent the too easy escape of the spores.

One series of mosses has the peristome long; the teeth stand nearly erect with the points touching or interlaced so as to form a kind of cage over the mouth of the capsule, thus protecting the spores from too weak a wind and allowing them to be blown away gradually a few at a time, and by high winds only. Such are *Dicranum, Campylopus, Leucobryum, Grimmia, Ceratodon, Symblepharis* and others.

The peristome cannot protect the spores from the wet, and in most of this set the capsule, on a long curved stalk, droops downwards with the mouth towards the ground.

In another series the peristome consists of filiform, slightly hygroscopic teeth, distinct from each other or united at the base by a membrane. In *Trichostomum* and *Dawsonia* the teeth are nearly straight, but in *Tortula* they are twisted into a spiral which, in damp weather, twists tighter and closer over the mouth of the capsule. The former two genera have too weak a peristome to resist strong winds, and generally grow in sheltered hollows. *Tortula* has a stronger peristome, and grows on walls and other exposed spots. Two species occurred in Fernando de Noronha.

In a third group the teeth are more or less hygroscopic, opening when dry and closing when wet. In some genera, *Phyllogonium* and *Blindia*, the teeth when wet never get beyond an erect position. In *Fissidens* and *Cryphaea* they attain a horizontal position and curl the points inwards. In *Orthotrichum Zygodon* and others they reflex the peristome till the backs are appressed against the capsule. In these the peristome is beautifully adapted to prevent the spores being blown away in wet weather, but there is nothing to prevent

their being blown away in one direction by a strong wind. These mostly inhabit sheltered spots in forests.

Capsule with Double Peristome.—In these the outer peristome is hygroscopic, closing over the mouth of the capsule in wet weather and opening, spreading outwards with incurved teeth, when dry. The inner peristome is not hygroscopic, but on the opening of the outer one the interior projections, as well as the points of the teeth, get entangled in the perforations and cilia of the inner peristome and drag it open, often quitting their hold with a jerk which throws out the spores. Such are *Bryum*, *Isothecium*, *Hypnum*, *Rhizogonium*, *Racopilum*, *Mnium* and others. They chiefly inhabit plains and forests. Nearly all have the capsule deflexed or inclined on a long stalk.

The aquatic *Fontinalis* has the inner peristome in the form of a cone with square perforations which prevent the spores being washed out too quickly.

In *Funaria* the double points of the teeth of the outer peristome are connected with a disc which in time falls away; the inner peristome has narrow teeth which are hygroscopic and curl outwards when dry after the rupture of the disc. The capsule is pendulous on a hygroscopic stalk which, when curled or uncurled, keeps the mouth pointing downwards and thereby protects the spores from rain. Thus at first the strong united peristome enables it to distribute the spores in small quantities in high winds, while afterwards the mouth opens wide and allows all the spores that still remain in the capsule to be blown away.

Funaria hygrometrica is a very widely dispersed moss which seems to be especially fond of charcoal. Its spores must occur in vast quantities in the air, for I observed in the Malay Peninsula, wherever a fire had been lit and wood burnt, this moss would appear in abundance on that spot in a few weeks, and indeed it is reported to appear in this way almost all over the world.

Hepaticae.

The Liverworts (*Hepaticae*) are mainly dispersed by spores, like mosses, but are by no means so abundantly diffused.

D. H. Campbell (in the *New Phytologist*, 1907, p. 203) gives an account of the distribution of *Hepatics*, and notes some remarkable distributions, as of *Calycularia* with 3 species in Java, 1 in the mountains of the East Indies, and 1 in Arctic Siberia.

These peculiar distributions may be due to want of careful collecting, as few ordinary botanical collectors search for these plants, many of which are small and easily overlooked.

That they reach oceanic islands later than mosses is clear, for while there were two mosses in Krakatau by 1886, the first *Hepatic* (*Anthocerotes*) did not arrive till 1897, and Campbell says he spent a whole day searching for them in 1906 and could find none.

They are very scarce in the more xerophytic islands. In Fernando de Noronha I found only 1, *Riccia Ridleyi*, and in Christmas Island only 2 species of *Ptychanthus*. In many islands no attempt seems to have been made to collect them, but I give a table of such islands as I have found records of, to compare with the abundance of mosses therein :—

	Hepatics.	*Mosses.*
Canaries	63	116
Ascension	10	25
St. Helena	20	23
Tristan d'Acunha	11	26
Marion Isles	6	24

	Hepatics.	*Mosses.*
Kerguelen	26	155
Amsterdam and St. Paul's	4	28
Christmas Isle	2	15
Krakatau	1	19
Admiralty Isles	6	14
Cocos-Keeling	—	1
Juan Fernandez	15	23
Fernando de Noronha	1	4
Bermudas	6	8
Campbell Island	37	41
Auckland	70	40

Kerguelen Island is remarkable for only possessing 21 *Phanerogams* and 6 vascular *Cryptogams* against this wealth of mosses and hepatics, and the Auckland Isles for being richer in hepatics than mosses.

Many of the terrestrial hepatics are dispersed by the floating of their gemmae in water. Yeates states that *Fegatella conica* (*Marchantiaceae*) occurs on bridges and banks of rivers. The plants do not fruit where they are constantly and prolongedly submerged, but on places like arches over streams, and he therefore concluded that they owe their distribution to water carriage of both spores and detached plants. *Metzgeria* has thallidia transported by water and conveyed from higher to lower levels on the same tree trunk, and from one tree to another.

Yeates (in the *New Phytologist*, 1908, p. 167) seems to discredit the wide dispersal of hepatics by spores, at least in England. He says that:— "Prof. Campbell is quite right in discounting the prevalent assumption "that because of the lightness of spores of hepatics, they are specially fitted "for rapid dispersal by wind," and agrees with H. D. Humphrey, cited by Prof. Campbell, that the spores not only quickly lose their power from desiccation, but that no important number of them ever germinate at all owing to unfavourable conditions surrounding the parent structure. He mentions *Dumortiera irrigua* (a plant of a widespread tropical genus), which only occurs in Britain in Devonshire, Hastings and Ireland, and says that since the plants belong to a widespread tropical genus, this fact seems to indicate that they owe their present distribution to Miocene and Pliocene times when Britain and Ireland were united, and when the climate, especially during the earlier Miocene and Pliocene times, must have been of a tropical nature.

Of *Marchantia polymorpha* and *Lunularia*, he says the distribution is to be explained by the asexual production of gemmae. These bodies, coated as they are with adhesive mucilage, become readily attached to the coats of animals. This view will account for the presence of *Lunularia* in those situations more or less frequented by rats, as in the neighbourhood of gullies and sewers, as well as in the more open situations to which the gemmae may have been conveyed attached to the feet of birds. I would add, in the case of *Marchantia*, the possibility of their being conveyed also by human feet, as the plant is very common on the bare ground on estates in the Malay Peninsula. *Marchantia polymorpha*, and its form or sub-species *M. tabularis*, is extraordinarily widely scattered and common, being found in Europe, India, China, the Malay Peninsula, Africa, Australia, New Zealand and America, also in the island of Kerguelen, Tristan d'Acunha, St. Helena, Ascension, St. Paul and Gough Island.

There is no doubt that in some places it is transported in pots or soil with other plants, as is *Lunularia*, as McVicar states in the distribution of *Hepaticae* in Scotland. But it is quite impossible that it should have been

conveyed by human agency, rats or birds, to such places as Kerguelen, Tristan d'Acunha, or St. Paul or Gough Island. These islands have been very rarely visited by man, and the only birds which visit them are sea-birds, which do not haunt the places where these hepatics grow. The same remarks apply to the large number of other hepatics which occur in Kerguelen and such islands, and also to the great abundance of them in the tropical forests of Asia and America, and especially to the numerous epiphyllous hepatics which are so abundant in Brazil and other forests of the tropics. It is therefore only possible for these plants to have reached their positions as spores transported by the wind.

I take it, however, that Yeates's remarks refer only to these species in England. It is quite conceivable that most of these hepatics are relics of an earlier and more tropical period, which have now almost ceased to reproduce themselves by spores, owing to a cooling of the climate, and have only persisted because of being able to propagate themselves asexually by the gemmae in our cold climate. I shall have occasion later to mention some higher plants in which, owing to change of environment, the reproduction is perpetuated by vegetative organs only.

Campbell writes (*New Phytologist*, 1907, p. 211) on this subject:—

"The ready distribution of ferns by means of their spores has often been "cited, but with these, as with hepatics, there are great differences as to the "ease of distribution. Ferns with thick-walled spores are readily disseminated, "as the spores retain their powers of germination for many months, and even "years. But there are other ferns, such as *Hymenophyllaceae* and *Osmundaceae*, "whose spores quickly perish unless they immediately have the conditions "necessary for germination."

These ferns may well be compared to hepatics of wide distribution whose spores are not fitted for a wide dissemination. He attributes the wide distribution of many species to their great antiquity, the *Hymenophyllaceae* and *Osmundaceae* being known to be plants of an early period. But *Hymenophyllum* and *Trichomanes* (*Hymenophyllaceae*) have quite frequently reached oceanic islands which were never connected with the mainland. By 1919 *Trichomanes humile* had appeared at Krakatau, and before that had come the hepatic *Anthoceros*. *T. tenerum*, a South American species, has reached Tristan d'Acunha (5,520 miles). *T. saxifragoides* (of Polynesia and eastern Malay Isles) grows in Amsterdam Island, *H. capillaceum* is found in St. Helena, *H. aeruginosum* is endemic in Tristan d'Acunha, and the Polynesian and South African *H. obtusum* is found in Amsterdam Island.

There can be no doubt that these ferns owe little or nothing of their distribution to their antiquity, and the same may be said of hepatics and all the lower cryptogams. The spores drift far away, many hundreds of miles, and practically their distribution of the species is due to the distribution of suitable habitats.

It is thus perfectly clear from these records that *Hepaticae* and *Hymenophyllaceae*, though their spores are thin-walled and not long-lived, do spread about the world by their wind-borne spores. That hepatics are not more abundant in some of the islands is no doubt due to the fact, as stated by McVicar, that they cannot stand competition with mosses except in the most humid parts of woods, and their distribution is largely a matter of rainfall.

The hygrophytic nature of a country may vary from century to century, and these hepatics now found in remote isolated spots may have been formerly much more common and more widely distributed between their present habitats, the intervening areas having become in the lapse of time more unsuited for their growth.

LICHENS.

Lichens are flattened or crustaceous, foliaceous or erect branched plants growing on rocks, trees or the ground in all parts of the world, but are certainly more rare in the tropical rain forests than in the colder climates. I observed in the Botanic Gardens in Singapore that lichens frequently grew on the smooth bark of such trees as *Ficus Benjamina*, but if the bark became cracked or in any way roughened, soil particles would be washed into the depressions, and moss would begin to grow, and, spreading over the lichens, would very soon quite exterminate them. This is certainly one reason why in the forests we get abundance of mosses to the exclusion of lichens. The organs of fructification of lichens are the *Apothecia*, which are sometimes sessile or stalked and sometimes sunk in the thallus, discoid, linear or globose, or when immersed in the thallus they form a pouch (*conceptacle*). They consist of a mass of sporanges (*thecae*) containing spores. Mixed with the sporanges are usually a number of filaments thickened at the top and known as paraphyses. Each sporange contains from 1 to 8 spores usually, but 20 to 100 spores may be contained in one. The spores are very minute, ellipsoid, fusiform, oval, or oblong-cylindrical, from ·00027 to ·00003 of an inch in length, according to the number in the sporange. They are thus extremely light, and are ejected by the pressure of the paraphyses and borne away by wind, rain-wash, or attachment to insects.

A case of dispersal in *Sagedia microspora* is described by Miyoshi, in which entire fruits, small round perithecia, are dislodged and carried away by the wind. The addition of water causes them to swell enormously and eject the spores.

Miss A. Lorrain Smith (in " Lichens," p. 256) gives a number of instances in which portions of the thallus or buds from it are dispersed by wind, and when blown to a distance settle down and develop into fresh plants.

In crustaceous lichens the thallus becomes cracked into small areolae, which by unequal growth become lop-sided, or form little warts or excresences on the surface. Eventually the thallus becomes detached from the rock or bark, and the particles are carried away by wind or water.

In foliaceous lichens many form *isidia*, easily detached out-growths from the thallus. Butler considers the coralloid branchlets occurring in compact tufts on the thallus of *Umbilicaria pustulata* are of immense service in propagation.

Fruticose lichens are often abundantly fruited, and in others *Soredia* (one or more green algal cells enclosed in fungal hyphae) are constantly developed, and *Usnea*, *Alectoria* and many *Cladonias* are mainly propagated by these organs, which are peculiarly liable to be broken off and dispersed by wind or rain.

Erratic lichens.—In these there is a tendency for the thallus to develop excrescences of nodular form which easily become free and drift about. The best known is *Lecanora esculenta*, the Manna lichen, which at first grows as a crust on stones, chiefly limestone, and eventually cracks and becomes detached, the edges being curled in so as to form a kind of light ball. Kerner gives the weight of those as big as a hazel nut as 0·34 of a gramme (about 5 grains), so that these balls are readily blown about across the deserts. These Manna lichens (*L. esculenta*, *L. desertorum* and *L. Jussufii*) have an immense distribution, occurring from Persia through Arabia to Algeria and South Europe. Rain-wash, however, plays also a large part in the dispersal of the Manna lichens.

Other wandering lichens of the same type are various species of *Parmelia* and several other crustaceous lichens. *Parmelia revoluta* var. *concentrica* is a spherical unattached lichen which rolls about on the Dorset and Sussex Downs. The balls are spherical or more or less flattened. They are from ½ inch to

3½ inches through. The edges of the overlapping lobes make the balls rough, so that they readily become entangled in long grass or on rough ground surfaces.

G. J. Peirce (in "On the Mode of Dissemination of *Ramalina reticulata*," *Bot. Gaz.*, xxv, 404, 1908) found that *Ramalina reticulata*, of which the fronds are an open network, was mainly distributed by the tearing of the lichens in high winds. This takes place in the winter rains, when not only is the lichen wet and soft in texture, but the trees are bare of leaves, when the drifting bits of thallus can be blown (and attached) to the trunks and branches.

Schenck (in Trans. Acad. Soc. St. Louis, viii, 189) made a series of observations on the dispersal of the *Usneas* in North America in places where they rarely bear Apothecia. The high winds break and disperse them when they are wet. They generally grow over spruce and pines, because the drifting filaments are most easily caught and entangled in the short pine needles. The successive wetting and drying cause them to coil and uncoil, resulting in a tangle impossible to unravel, which holds them firmly to the spot. He states he finds by experiment that a wind of not less than 50 miles an hour is required to blow off pieces of the lichen, but it is probable that a lighter wind would be effective. *Usnea barbata* is very widely spread over the world, and apparently chiefly by wind, as Apothecia are not common except on the exposed mountain tops as in the Malay Peninsula, where it is known to the natives as Tahi Angin—the excrement of the wind. It occurs in Christmas Island, as do 2 species of *Ramalina*.

Fungi.

Fungi are plants consisting of a vegetative portion, Mycelium, and the fructification, which varies very extensively according to the group to which the species belong, and the spores, which are, as in other cryptogams, very light and minute, and often produced in vast abundance.

The fungi can only be dispersed by portions of Mycelium or by the spores. Mycelium must be but rarely dispersed by wind to any great distance. Small detached fragments perish quickly, and larger pieces are too heavy to be carried through the air. The Mycelium is also less resistant to unfavourable conditions than are the spores.

It is, however, certain that the Mycelia of some of the Hymenomycetes are carried about the world in timber, and after a time fruit, as is certainly the case with *Schizophyllum commune*, *Polystictus igneus* and *Guepinia spathulata*, which frequently appear on imported timber and are now scattered all over the world. It is possible, too, that other dead-wood fungi have been conveyed thus to other parts of the world.

Spores.—Fungal spores are very often long-lived and can withstand drying or extremes of heat and cold. The spores of the bunt of wheat (*Ustilago caries*) have germinated after 8 years, and have been kept in a solid block of ice for 3 months in Canada without injury, although more than once the temperature fell to 28° F. They can be killed by immersing them in hot water at 130° F. for 10 minutes, and those of the Yellow Rust of India by 5 minutes immersion in water at a temperature of 120° F. When dry they can resist higher temperatures. There are exceptions to this, however, as the summer spores of the downy mildew are unable to survive after 24 hours drying.

The amount of spores produced by some of the fungi is enormous. Butler gives the following :—

Psalliota (Agaricus) *campestris* (mushroom)	1,800,000,000
Coprinus comatus	5,000,000,000
Polyporus squamosus	11,000,000,000
Lycoperdon Bovista	7,000,000,000,000

Movement of Spores.—In *Ascomycetes* there is a certain amount of expulsion of the spores from the Asci (explosively treated of under "Explosive Fruits," on p. 674), but, as it has been said, the flight of the spores in most cases is due to air currents.

R. Falke gives a curious theory for the method of spore dispersal in *Hymenomycetes*. He says that the fruit bodies (pileus) actually produce heat so as to warm the layers of air beneath the pileus. This warmth produces convection currents in which the spores are borne away, and suggests that the Agarics produce fleshy pilei to induce maggots to feed on them, because such animals respire quickly and raise the temperature, which thereby increases the convection currents. Butler, however, suggests that these heated currents would hardly be sufficient to make any material difference.

Height of Flight of Fungus Spores.—The very minute and light spores may be readily transported through the air and may be carried by air currents to a great height.

Observations on the height to which they could ascend were made by the officers of the Aerial Investigation Bureau of the United States Department of Agriculture in 1921, with the aid of aeroplanes. They exposed mechanical traps of microscopic slides smeared with vaseline at different altitudes, so as to catch any floating spores.

At 10,000 feet, and in some cases higher, they caught Rust spores of wheat, *Puccinia triticina*, and numerous spores of *Helminthosporium*, *Alternaria*, *Cladosporum*, *Cephalothecium* and *Ustilago*. Spores of *Alternaria* caught at 11,000 feet altitude germinated readily (Stakman, Henry, Christopher and Curran, in *Journ. Agric. Research*, xxiv, p. 599). They say that many spores of fungi, conidiophores, pollen grains, glumes of grasses and small insects were caught on glycerine slides. Besides the above-mentioned, they state that *Tilletia* and *Scoletotrichum* spores were recognised. Two spores, probably of *Puccinia triticina*, caught at 16,500 feet altitude, and *Uredospores* and *oecidiospores* of *Puccinia graminis*, caught at 7,000 to 10,000 feet altitude, readily germinated, as well as those of *Alternaria*.

The spores are often produced in immense abundance. Butler says:—

"A small spore-horn of *Endothria parasitica*, the chestnut-bark fungus, "may contain 115,000,000 spores. A bean pod affected with bean anthracnose "(*Glomerilla Lindemuthianum*) may produce in the season 500,000,000 to "1,000,000,000 spores. *Lycoperdon bovista* (the large puffball) may contain "7,000,000,000 spores, and the common mushroom (*Agaricus campestris*) "can shed 40,000,000 per hour. Many spores have fine spines on the outside, "and the anthracnoses liberate the spores with a mucilage which is adhesive on "drying, and by these means the spores are attached to objects with which "they come in contact." (Butler, "Dissemination of Fungi," *Mem. Dept. Agric. India*, ix, 2.)

Weston ("On the Production and Dispersal of Conidia in Sclerosporae of Maize," *Journ. Agric. Researches*, xxiii, p. 23) says of *Sclerospora*: The conidiospores develop during the night, and the conidia mature most abundantly at about 2.30 a.m., and are set free by active ejection from the sterigmata. Estimates of the number of conidia produced on one plant of Maize in one night ranged from 758,003,400 to nearly 6,000,000,000. This continues night after night for some months. Their dispersal is chiefly effected by wind. Slight air currents and strong breezes are important. Violent gales do not promote the copious production of conidiophores, but sweep the conidia to great distances. Drops of dew or rain also disperse them from leaf to leaf, and agents of minor importance are surface water, insects, and moist infected soil. Human agency also plays a not unimportant part in their transit from place to place.

C. R. Orton (in "Seeds as Carriers of Disease," *Journ. New York. Bot. Gard.*, xxvii) says that seeds (of cultural plants) will carry fungi, bacteria and nematode worms, and the mosaic and yellow diseases, the life-history of which is not known. Fungi may be carried, attached externally on the seeds as spores, in such species as the stinking smut of wheat (*Tilletia tritici*) and covered smut of *Sorghum*, and internally as mycelium in loose smut of wheat (*Ustilago tritici*), bean anthracnose (*Colletotrichum Lindemuthianum*), and *Diplodia* of corn, *Glomerella*, etc.

Flight of Spores.—It has been shown that spores soar to a great height, and many must fall at a considerable distance from where they started. Butler (in "Researches on Fungi") states that they fall at from 0·05 to 5 mm. per second in still air. When we consider the vast distances at which dust from volcanoes and dust carried by desert storms can travel, the distance to which these light spores can go would appear to be very great. Butler, however, shows that the actual distances to which spores of a parasitic fungus have spread is not as great as might be expected. Spore-traps both in Germany and Russia remained free of smut spores beyond 250 yards from an infected field. *Coliospermum euphrasiae* seems to reach the islands off the north-west German coast, and other cases are recorded of the occurrence of one stage of the life of these fungi from 5 to 8 miles from the place bearing the alternate stage.

In dealing with injurious fungi he shows that in the greater number of cases these pests have not been spread by the wind for long distances, but have been spread almost invariably by human agency, the attacks being shown to be due to the introduction of diseased plants. Thus he cites the Chestnut bark fungus as having been unable to leap a 30 or 40 mile belt in the Catskill Mountains in North America, the belt being free from Chestnut trees. The blister blight of tea (*Exobasidium vexans*) was known in Assam in 1868, but did not reach Darjeeling for 40 years, viz., in 1908, and has not yet reached the nearer and equally suitable district of Cachar and Sylhet.

The Godavery Palm disease (*Pythium palmivorum*) appeared about 1890 and spread among the Palmyra palms (*Borassus*), killing in many parts from 50 per cent. to 75 per cent. Its extension was continuous at about 1 to 3 miles a year. Over 1,000 acres were attacked in 1905, but though the spores are sometimes formed in situations freely exposed to the wind, they have not been able to travel through the air for even a 24 hours' journey. Further evidence is given in the case of the genus *Uromyces*, of which in Europe there are 119 species. Of these, only 3 species and 2 doubtful ones have yet reached America, while of the American species, out of 249 only 1 has reached Europe. All the plants thus exchanged are parasitic on cultivated plants, and have undoubtedly been transported by human agency. However, it seems clear that in many cases fungi, especially the *Basidiomycetes* and *Myxomycetes*, are very widely distributed, and cannot have reached the oceanic islands in any other way than through their spores having been transported by wind.

In Christmas Island, Lister obtained 3 species of fungi before any human beings had arrived at the island—*Polyporus australis*, *P. conchatus*, and *Stereum lobatum*. Andrews and I, coming later, secured 47 more species, of which 2 were endemic. Some few of these may have arrived on timber, but most of them could not have come by any human agency. On Krakatau 3 species are recorded in the second expedition. Two of these (*Polysticti*) might have arrived on floating logs, but 1 (*Hygrophorus*) certainly could not, nor could the Mycorrhizas of the Orchids on both these islands (*see* "Seeds of Orchids," p. 44), nor the *Myxomycetes* of Christmas Island (3 species). From Kerguelen Island there are 9 fungi recorded, *Agarici* 5, *Coprinus* 2, *Peziza* 1, *Sphaeria* 1. From Marion Isle 2 *Agarici*. From Tristan d'Acunha 1 *Agaric* and a *Hypoxylon*.

The distribution of fungi is even less known than that of mosses and hepatics,

as, except the woody ones, they are rarely collected. Some, like *Saccharomyces*, appear to be floating in the air all over the world in immense abundance, others are extremely local However, the complete area of distribution of most species is as yet unknown.

ALGAE.

The minute blue-green algae and bacteria are widely diffused through the air, and play an important part in adapting new soil for the growth of higher plants. Ernst, in the account of the vegetation of Krakatau, says :—

"Three years after the volcanic outburst, dark green gelatinous layers "of blue-green algae (*Cyanophyceae*) were found on the surface of the pumice "and ash and on the loose stones in the ravines of the mountain slopes. "These were correctly regarded by Treub as affording a satisfactory nutritive "medium for the germination of the spores of *Cryptogams* and the seeds "of Phanerogams."

A new aerobic nitrogen fixing bacterium, *B. Krakataui*, was found, and *Bacterium radicicola*, the well-known nitrogen fixing bacterium, which lives symbiotically in the roots of *Leguminosae*, had been carried to the islands by wind agency.

Brun (in *Bull. Soc. Microscop.*) records the fall of *Chlamydococcus pluvialis*, mixed with organic remains and fine sand, at Ouersin in Morocco, from the Sahara, brought by wind.

Comparatively little has been recorded as to the distribution or dispersal of terrestrial algae, but it is quite clear that numbers of them or their spores are diffused throughout the atmosphere and may be drifted to vast distances by wind currents.

PART III

FRUITS AND SEEDS DISPERSED BY WIND BY SPECIAL ADAPTATIONS

FRUITS may be so modified that their mere lightness causes them to be readily drifted away by the wind either by the dilation of the capsule into a bladder-like structure, as in *Sutherlandia*, etc., of the *Leguminosae*, or *Staphylea* (*Staphyleaceae*); or the whole fruit may become papery and expose a large surface, in proportion to its weight, to the wind, as in *Isatis* (*Cruciferae*) or *Derris* (*Leguminosae*); or the angles of the carpel, or of the whole fruit, may be drawn out into a wing, as in *Acer*; or again, some part of the floral structure in inflorescence may be persistent, or accrescent, and form a wing for the flying fruit. Thus we have fruits winged by the bracts, pedicels, sepals or petals, which in many cases are enlarged during the fruiting period by continued growth (accrescence).

In most of these cases the continued growth takes place after the fall of the corolla and during the development of the fruits and seeds.

In the case of the *Dipterocarps* the sepals during the flowering period are short and inconspicuous, but after the fall of the corolla they continue to grow till they attain a considerable size. In many cases only one out of four or five sepals continues to grow, forming eventually a one-winged fruit. Indeed, it is not usual for all the sepals to continue their growth to an equal extent, as there are certain advantages to be gained by a reduction of the number of wings. A two-winged fruit actually flies further than a four-winged one.

The winged fruit is almost invariably one-seeded, rarely ever two-seeded; even though the ovary may have contained several ovules, one only is developed into a seed. Of course it is easy to find cases of flying fruit which do contain more than one seed in plants in which the evolution from a many-seeded capsule or pod to a one-seeded flying fruit is developing. We see this in the case of Honesty (*Lunaria biennis*), some of the *Acacias*, and in Laburnum. As evolution is still going on, it would be strange if we did not meet with examples of intermediate stages.

This reduction of the seed in number causes a more satisfactory dissemination, as it prevents two seedlings coming up too close together, in which case only one, or perhaps neither, would survive.

The seeds are usually flattened, at least in the case of the flattened pod or capsule, and smaller and lighter than in the cases where they are merely dispersed by ejection from the capsule.

The wings are of various shapes, but are always either papery or thinly, rather stiffly coriaceous—in any case quite light.

As a rule, the fruits are brown, green or whitish in colour, and in *Congea* and *Bougainvillea*, though the bracts during the flowering stage are bright pink, which tends to attract insects to the smaller and less conspicuous flowers for the purpose of fertilisation, in the fruiting stage they lose this bright colour and become dull light brown or whitish in appearance. In some cases, however, the wings take on a showy red colour (*Dipterocarpus*, *Shorea*, *Melanorhea*), and more rarely a bright yellow (*Pteleocarpa*). Conspicuous red or yellow colouring in fruits usually indicates that the fruit is destined for seed-dispersal by birds, which are attracted by the bright colouring, and this is described in the chapter on that subject on p. 390. In the case of coloration of winged fruits this is not so, as birds do not eat them, the bright colours being analogous to the autumnal tints of the foliage of many plants, or the red or purple colouring of the bracts (glumes) of many sedges or grasses.

In *Dioscorea* and *Begonia* the carpels are strongly winged in many species, but the winged fruit remains attached to the plants and is not drifted away by the wind. The seeds of *Dioscorea*, however, are winged, and the evolution of the three carpellary wings seems mainly to be required to give room to the seed wing. In *Begonia* the fruit dehisces between the wings and releases the tiny seeds, which, when fallen, are partly dispersed by wind and partly by rain-wash. The carpellary wings may, however, act as vanes blown by the winds, so that after dehiscence the seeds may be further shaken out of the capsule by the action of the wind swaying them about, and possibly the same may be the case in the long pendent sprays of capsules in *Dioscorea*.

Far the greatest number of plants with winged fruits are either trees or lofty climbers. It will be noticed that even in Europe the greater number of large trees have winged fruits or seeds, e.g., *Elm*, *Ash*, *Sycamore*, *Maple*, *Hornbeam*, *Alder*, *Birch*, have winged fruits, while *Pines* and *Larch* have winged seed, and *Poplars* and *Willows* plumed or woolly seeds. The remainder, usually smaller trees or shrubs, have drupes or berries, the seeds of which are disseminated by birds, or *Oaks* and *Chestnuts* chiefly dispersed by mammals. In tropical forests, where the trees are much more lofty and crowded, and where the woody climbers (Lianes) climb to nearly as great a height, a very large proportion have either winged seeds or fruits.

Trees of a great height, 150 to 180 feet, and the loftiest climbers, seldom have drupes or berries destined for dispersal by birds. Fruits disseminated by birds are nearly always small, and would not be sufficiently conspicuous among the mass of foliage of these gigantic trees or the lianes to attract the birds.

A certain number of trees of great size have large and heavy fruits which are dispersed merely by falling from the great height and rolling along the ground, or are dispersed, when fallen, by rats or other animals which carry them off; but when the fruits are small enough, the action of wings aided by a wind seems to be the most efficient method of carrying the seed from the immediate vicinity of the mother-plant and preventing their lodging among or on the mass of foliage, and allowing them eventually to come to rest in more or less open spaces between the young trees and bushes, where they can eventually germinate and develop into fruiting trees. Very few small trees or bushes or low climbers possess winged fruits, but a certain number of

herbs have fruits variously winged to aid in the seed dispersal, and these are mainly blown along the ground or into rivers and then further dispersed by water. Naturally such plants are inhabitants of open country, mountain-sides, steppes or deserts.

It must be remembered that the flying apparatus, whether wing or plume, of fruit or seed only functions in a current of air. If the air is quite still, the fruit or seed falls directly to the ground. This applies even to the wonderfully light-plumed seeds of *Epilobium*. Even in a closed room the mere upward current of the hotter air from the fire causes them to rise to the ceiling, and the slight current's from door to closed window attracts their flight in that direction. In any place where there is no current of air they fall slowly but nearly directly downward. Placed in a tumbler which is then inverted, they fall immediately to the ground.

In the case of the heavier-winged seeds or fruits, the fall in still air is direct. Unless there is a fairly strong wind, heavy fruits fall as if unprovided with any means of flying. Air currents of a strength varied according to the weight of the fruit or seed, and in proportion to the area exposed to the wind, can carry one of them to any distance from the point of fall. The stronger and longer the gust of wind which strikes the falling seed, the further it is carried.

In the case of winged fruits like those of the *Sycamore*, or of winged seeds, as of the *Pine* trees, the greater part of the crop, even when winds are strong, falls near the tree and too close to survive. Some, however, dislodged by a violent and long-continued gust, will fly a very considerable distance from the tree. It is these only which carry on the migration of the plant, so that in estimating the distance that a plant can move onwards in a given time, it is necessary to note only the furthest flown seeds.

When a seed or fruit thus reaches the ground, its travels are not necessarily ended, as under favourable circumstances in open ground it may be blown still further along the ground by following blasts, and frequently travels a greater distance in this way than in its first flight from the tree, as will be shown later. The position of the tree from which the seed is blown is another factor. The seeds or fruits from a plant on a mountain top will go much farther than from one on a plain, and not unfrequently winged fruits blown into a river continue to be blown further along on the water, for most of the wind-borne fruits float for some time, and I have even seen fruits of Dipterocarps blown up stream against a strong current by a high wind acting on the wings projecting above the water.

The importance of the wings and plumes of fruit and seed is to delay the fall, for as long as it is in the air the wind can act upon it, and it is for this reason that the wings are often found to be oblique, causing the fruit to rotate rapidly as it falls, thus making its fall so much slower that it remains longer under the wind, the influence of which has dislodged it from the tree, and which carries it a further distance before it reaches the ground. The longer it takes to reach the ground and remains under the influence of the wind, the further a seed or fruit will go.

It is for this reason that the winged seeds and fruits do not fly as far as the plumed ones, while spores and dust seed, so light that they float in the air, go further than plumed seeds.

WINGED SEEDS AND FRUITS: DISTANCES OF FLIGHT.

I am giving here the distances to which winged fruits and seeds can actually fly from the tree in a tolerably strong breeze, and can be drifted along by the wind after falling. The furthest distance of each fallen fruit or seed has been

taken, for this is what counts in dispersal. A very large proportion of these fruits, even when well provided with flying organs, will fall close to the tree, and unless other gusts of wind carry them further along the ground they are wasted, for though they may germinate they soon perish.

There is a good deal of evidence to show that under favourable circumstances, such as in a case where the trees are growing on exposed mountains at some elevation with a flat plain below, the seeds or fruits will fly to a much great distance than if they are in flat country, and it will be understood from the accounts given here of the strong action of wind in deserts, etc., that the actual migration of seeds and fruits in this way may be much accelerated under such favourable conditions. I would point out here that in forests big trees grow at a distance of about 30 yards apart, and smaller trees can grow between them, but if of the same species they do not generally attain the size necessary to produce fruit. I have seen seedlings of *Shorea* and *Dialium* in forests, too close to the parent tree and crowded by other bushes, remain at from 5 to 12 feet tall for over 20 years, and of course they could never reproduce themselves, as they do not fruit till they are 30 or more feet in height.

In the following list I have taken the measurements in most cases from observations of my own made in Kew Gardens, Surrey, and in the Botanic Gardens of Singapore. The distance of fall given is from the top of the tree or climber, the height of which is given to the ground (as the height from which the fruit starts is an important factor), and as far along the ground by following gusts of winds as I could with certainty discover. The winds at the time the flights were measured were strong, but never very violent, and in some cases the flights represent the fall-flight of the fruit with no continuance of movement along the ground. This was especially the case where ground-wind was wanting, although many winged seeds, such as those of pines, do not seem to be affected by ground-wind, as after falling they lie flat on the ground. The furthest distance of any fruit or seed which was fertile was taken, as the most distant fruits are the ones which carry on the migration of the species. In many trees, such as the *Shoreas*, the first fallen fruits are sterile and much lighter than the fertile ones, so that it is possible for them to fly further; after these have fallen the fertile ones fall, and it is the measurements of the flight of these that I have taken.

Under exceptional circumstances the distance which these flying fruits may go is probably greater, but it will be noticed that in nearly all the big trees the distance ordinarily flown is over 30 yards, which is the flight-distance required for the evolution of a full-sized tree in the forest.

It is quite clear that the normal distance of flight of winged fruits and seeds is usually not sufficient to allow of their crossing an arm of the sea of more than 1 mile or so, and this is proved from the distribution of this class of tree which is quite absent from oceanic islands, unless, as is sometimes the case, the seeds can float and are dispersed by sea after being blown into the water, as in *Gyrocarpus*, *Casuarina*, *Melochia*, etc. In this the contrast with plumed seed and spores or dust seed is very marked.

FLIGHT OF WINGED FRUITS AND SEEDS.

		Height of Tree or Climber.	Distance.
		Feet.	Yards.
Shorea leprosula	(*Dipterocarpaceae*)	150	50–98
„ *macroptera*	„	80	20–40
„ *gratissima*	„	80	16
„ *rigida*	„	80	20
Anisoptera costata	„	80	6–15

		Height of Tree or Climber.	Distance.
		Feet.	Yards.
Terminalia subspathulata (*Combretaceae*)	..	100	36–46
Scaphium affine (*Sterculiaceae*)	.. ..	80	50
Koompassia malaccensis (*Leguminosae*)	..	120	61
Spatholobus ferrugineus (*Leguminosae*).	Climber	120	188
Cytisus laburnum (*Leguminosae*)	.. ..	15	70
Ptelea trifoliata (*Rutaceae*)	.. .. ..	15	80
Tilia dasystyla (*Tiliaceae*)	.. .. ..	20	18
Ventilago malaccensis (*Rhamnaceae*).	Climber	60	40
Acer pseudoplatanus (*Aceraceae*)	.. ..	50	40–93
„ *platanoides* „	.. ..	20	56
„ *campestre* „	.. ..	20	90
Ailanthus glandulosus (*Simarubeae*)	.. ..	30	300
Robinia pseudacacia (*Leguminosae*)	.. ..	40	150
Carpinus betulus (*Cupuliferae*)	.. ..	25	100
Ferula communis (*Umbelliferae*).	Herb ..	6	15
Dyera costata (*Apocynaceae*).	Seed	100	40
Fraxinus excelsior (*Oleaceae*) ..	.. ..	20	134
„ *oregana* „	.. .. ..	40	50
„ *ornus* „	.. .. ..	20	12
Pinus laricio (*Coniferae*).	Seed	60	80
„ *taeda* „	.. .. ..	100	100
„ *alba* „	.. .. ..	100–200	880
„ *contorta* „	.. .. ..	—	164

The last three pines from the U.S.A. reports on afforestation.

Pinus sylvestris (Robert Smith)	.. ..	—	886
„ (Flicke)	.. .. ..	—	72
Cedrus atlantica	.. ..	40	80
Betula alba (Smith). Fruit ..	.. ..	—	489

WINGED FRUIT.

Winged Fruit not Dispersed by Wind.

In the *Begonias* the capsule generally has from one to three wings developed at the angles. Except in one section where the fruit is baccate, it dehisces along the sides and releases a large number of minute seeds. The fruit is not detached from the plant until all the seeds are gone, and the wings apparently only serve to swing the capsule from side to side until all the seeds are released and so to scatter them more widely. They are always woodland plants, and many occur in dense forest. It is probable that as the fruit swings on its pedicel, and the seeds are released, they are blown further away by breezes through the woods. The genus is very widely spread, but is absent from most of the remote islands. *Hillebrandia* is found in the Hawaii Islands, and one species of *Begonia* in Fiji, and one in Socotra. Guppy says (" Naturalist in Pacific," p. 394) : " It is not easy to explain why a genus with such minute seeds, which " are apparently as well fitted for dispersal as those of Orchids, should have " such a limited dispersal in Polynesia."

I do not think they are light enough to be classed as dust seeds, but there is no doubt that they travel by wind and probably also by rain-wash.

The *Dioscoreas* also have winged fruits, which contain winged seed. Here, again, the fruit is not blown away by the wind, but continues to hang long after the seed is dispersed. The wing seems to have developed merely to afford room for the seed, although it may also play a part in helping to shake the seed free from the capsule.

Bladder Fruits.

In the plants with bladder fruits the carpel or carpels are thin-walled, papery and dilated, so that the whole fruit is comparatively large in proportion to the size of the seeds, yet so light and exposing so great a surface to the wind that the pod can be blown to a great distance through the air or along the ground. Like many of the wind-dispersed fruits, these fruits float readily in water, so that their dispersal may be effected by wind, by river or by sea. This combination of the two means of dissemination depends largely on the habitat of the plant. *Dodonaea viscosa*, *Cardiospermum Halicacabum*, both of which habitually grow on sandbanks or shingle beds by the sea, are partly dispersed by wind and partly by sea travel, while other species of both genera which live inland are merely wind-dispersed. *Sutherlandia* and the shrubby *Staphylea*, *Kleinhovia* and *Colutea* owe their wide dispersal mainly to the bladder fruits being blown into streams, along which they sail with the current (Pl. IV, fig. 7, *Sutherlandia frutescens*).

Colutea arborescens of India and *C. aleppica*, inhabitants of sand dunes and deserts, are undoubtedly dispersed entirely by wind driving the light swollen pods across the open country.

There can be no doubt that in most cases at least of the *Leguminosae* with light swollen pods the enlargement and thinning of the walls of the carpel were brought about by their adaptation to wind-dispersal, as a considerable number of these plants are the inhabitants of open plains, and their dispersal by water, streams, floods or sea, was a later phase of evolution. So it is more convenient to describe them here under wind-dispersal, and merely refer to them later under the account of sea and river-dispersal. Of many plants with bladder fruits, the natural history, their habits and habitats have not been recorded, and information on these and their actual methods of dispersal are quite unknown.

J. Buchwald (in "Der Verbreitungs-Mittel der Leguminosen des Tropischer Afrika," *Engler's Jahrbuch*, xix) gives a list of *Leguminosae* distributed by water, and includes among these several species of *Crotalaria*, a genus very largely represented in Africa, many of which have dilated rather thin-walled, parchment-like carpels; but in all the species I have seen wild, the pods do not break from off the plant when the seeds are ripe, but dehisce on the stems, and it is essential for a pod to be dispersed, as a bladder plant, that it should be detached before it dehisces.

I am at present quite ignorant as to what importance this dilation of the pod is to these *Crotalarias*. In most cases they are not sufficiently thin and light to allow of their being blown to any distance. Doubtless, whatever be the use of their dilatation of the pod in these plants, it may be regarded as a preliminary step in the evolution of a bladder fruit, such as that of *Sutherlandia* or *Colutea*, for should the light swollen pod of a *Crotalaria* be detached before dehiscence by the breaking of the pedicel, it would be readily blown away, and so could be classed as a bladder fruit.

It is certain that the small inflated pods of *Anthyllis vulneraria* and *A. Dillenii* are blown along over downs and open country by wind; *Astragalus caerulescens*, of the Somaliland desert region, a tall herb, has very thin, narrow, flat, papery pods, which are readily detached and blown away, and are probably so

dispersed. Of the genus *Lessertia*, *L. brachypus* and some other species of the veldt of South Africa have oval pods, very thin and flattened. The plants are shrubby, and some are spinous. The pods in these plants are mostly one-seeded, breaking off below the pedicel, and are doubtless dispersed by wind along the veldt; but in *L. benguellensis*, of tropical Africa, we find that the thin bladdery pods contain usually 3 to 5 seeds, and these plants grow in water or in sandy river-beds. The pods here are evidently first blown by the wind into the water and then drifted along. *Phaca alpina* and *P. frigida*.—Of these *Leguminosae* Massart states that the swollen pods are detached after they are opened, offering a large surface to the wind.

In many of the herbaceous *Leguminosae* the calyx is inflated in fruit, especially when the flowers are borne in a head or dense spike, such as *Anthyllis vulneraria*, in which the flowers are thus condensed. Here the calyx becomes white and papery, and contains at the base a very small pod of one or two seeds. *Dalea*, a genus of South American herbs or shrublets, has the flowers in a dense spike. The calyx becomes inflated in fruit, and the single seed is enclosed in an indehiscent pericarp.

In *Trifolium fragiferum* the small pods, each containing one or two seeds, are enclosed when ripe in very much swollen calyces, the portion which represents the upper two sepals being greatly increased in size, while the lower three sepals remain nearly unaltered. In *T. striatum* the pod is included in the dilated calyx.

The genus *Dodonaea* (*Sapindaceae*) contains a number of widespread species of shrubs or trees which in many cases possess bladder fruit. The carpels are swollen and thin-walled, usually two in number, but three-winged fruits occur. *D. viscosa*, the most widely-distributed species, is known in the form of a low seashore shrub and a tree 30 to 60 feet tall. The light bladdery capsule is easily transported by wind to some distance, but in the case of the seashore shrub it is more frequently sea-dispersed, and an account of it is given under that section (*see* p. 269). The fruit is, however, blown into the sea before it is floated away, and the inland forms (usually trees) are undoubtedly dispersed over the mainlands by wind (Pl. IV, fig. 8). Koorders mentions that in Java the inland form of *Dodonaea* can apparently travel for a great distance by its fruits being blown away by wind. He has seen trees of it on two volcanoes 30 kilometres (18 miles) apart, and none on the intervening low-lying plains. The inland Australian species with winged capsules are doubtless dispersed by wind over the sandy plains, as are the inland species of Hawaii and the tree forms or species we find in India and the Malay Islands. These latter, however, are also largely planted for timber, and there are forests of the plant in many parts of Java.

It does not necessarily happen that a large number of species occurring in one region with a smaller number in distant localities originated in the area containing the largest number; but in this case I should certainly suggest that *Dodonaea* originated in Australia, where there are some 20 or 30 distinct species, shrubby plants growing on limestone hills or open slopes. Of these, *D. ericoides* has unwinged capsules hardly four-angled. The capsules of *D. triangularis* and *D. aptera* are small, oblong, and somewhat quadrangular, while *D. ceratocarpa* has similar fruits with a horn-like process at the tip of each angle. *D. Campbelli* has thin, very short four-winged fruits, and from this it is easy to derive *D. viscosa*, in which the body of the capsule is much reduced in size and the wings reduced to 3 or 2. The apterous species abovementioned quite resemble those of more normal *Sapindaceae*, and merely dehisce, letting the seeds escape to be carried away by rain-wash or by rolling. *D. Campbelli*, with a thinner, more flattened body and larger wings, could easily be dispersed by wind, though not so satisfactorily as those of *D. viscosa*.

The Hawaiian species mentioned by Dr. Guppy are allied to *D. viscosa* and undoubtedly derived from that species.

It is quite possible that the tree forms of inland habit have evolved from the seashore form, and now are merely wind-dispersed again.

D. viscosa is treated again later under sea-dispersed plants, with some of Guppy's critical remarks given on the genus (*see* p. 269).

Cardiospermum (*Sapindaceae*) is a climbing, slender, wiry plant, of which *C. Halicacabum* is known as the Balloon Vine; but as the wide dispersal of this species is in the main due to sea-currents, it is dealt with in that section (*see* p. 269). There are, however, several other species in South America which are not maritime, and these are undoubtedly wind-dispersed. The fruits are bladdery-trigonous and inflated, with several seeds (Pl. IV, fig. 6).

Aitonia capensis (*Meliaceae*) is a low South African shrub with five-winged bladdery capsules 1½ inch across. It inhabits open deserts and sandy spots, where its capsules may readily be blown along by the wind. *Melianthus*, a genus of several low shrubs or stout herbs with a tall raceme of flowers (order *Melianthaceae* allied to *Sapindaceae*), possesses similar fruits, those of *M. major* being 1½ inch long, and of *M. pectinatus* 3½ inches in length. They are also South African plants inhabiting open country. The dispersal method of all these bladder-winged plants seems to be the same. The pods are blown across the open sandhills and sometimes into streams, where they drift some distance and eventually come to rest, the capsule dehisces, or it may be torn or split as it travels, and so releases the seeds. There is a tendency in all to a reduction of the number of seeds developed, to a single one, which, as I have shown, is the ideal method of dissemination. All the plants with such bladder fruits are natives of open country, where they can be readily disseminated, and a considerable number have been evolved in the veldt of South Africa.

Staphylea has a simple bladdery pod, like that of *Sutherlandia*. The plants are shrubs of Europe and temperate Asia. They are probably dispersed in much the same way, but there is very little evidence of their natural history available.

Bladder Wings.

In many fruits in which the sepals are enlarged they form a bladdery, thin papery covering to the fruit, light enough to support the fruit for a short distance when blown off the plant, but apparently most effective when the fruit, having alighted, is blown along the ground by the wind. The calyx is often merely inflated, usually much enlarged, and is hardly distinctly winged.

Physodium (*Sterculiaceae*) is a treelet 10 to 20 feet tall, a native of Mexico, in which the calyx is inflated and winged at the angles. In *Antigonon* (*Polygonaceae*), a slender climber from Mexico, Guatemala and Venezuela, the sepals in fruit are thin and papery; in *A. leptopus*, ½ inch long and ovate; in *A. guatemalense* the two outer ones are very wide and rounded, 1½ inch long and as wide; in *A. flavescens* the calyx is papery, but not as wide as in the two previously-mentioned species. They serve to lighten the fruit, and probably aid in its drifting along the ground, but can hardly act as a support in the air. *Gymnopodium*, an allied genus from Honduras, has also fruits of this type.

Alvesia rosmarinifolia is a Labiate in which the calyx in fruit is largely dilated, and no doubt is dispersed by wind. It is an under-shrub with a tall spike of flowers. Like so many of these wind-dispersed plants, the nutlets, normally 4 in Labiates, are reduced in this plant to 1 or (rarely) 2. Were the full number developed in a wind-dispersed plant, the whole 4 would probably germinate together and consequently perish from being too close

together, therefore 2 or (usually) 3 of the nutlets are not developed. A similar reduction of the number of seeds may be seen in the wing-fruited *Cruciferae* and in other groups.

Four-Angled Fruits.

Even heavy fruits with 4 low wings or prolonged angles of the carpels derive some benefit from this embryonic form of wing. Such fruits are those of *Halesia tetraptera*, some *Combretums* and *Terminalias*. The Silver Bells, *Halesia tetraptera*, is a bush about 5 or 6 feet tall, and has oblong fruits from 1¼ to 1½ inch long, the base rounded, the tip acuminate. There are 4 wings running from the base to the point, about ¼ inch wide in most fruits, but wider in others. They are stiffly cartilaginous. The fruits hang from the branches, and I found them after the heavy gales of January, 1924, as far as 40 yards from the bush. The wings or accentuated angles of this fruit, which is rather heavy, serve to lighten the fruit and to prevent its lying flat on the ground, so as to expose the upper edge to the wind. When it falls the fruit lies with one wing uppermost, and if it falls on open ground, being supported by the under-wings, the wind rolls it over and over, the wings acting as sails. The plant is said by Asa Gray to be a big tree in the mountain regions of North America. Some at least of the quadrangular-fruited *Combretums* are certainly river or sea-dispersed, but there is no doubt as to the value of the 4 raised wing-like angles of the inland species in aiding wind-dispersal.

Fruits with Several Lateral Wings.

Pentace (*Tiliaceae*) is a genus of very lofty trees, in the high forest in the Malay region, in which the fruit is winged, usually oblong in outline, and it is interesting to note that the number of wings varies much in the different species.

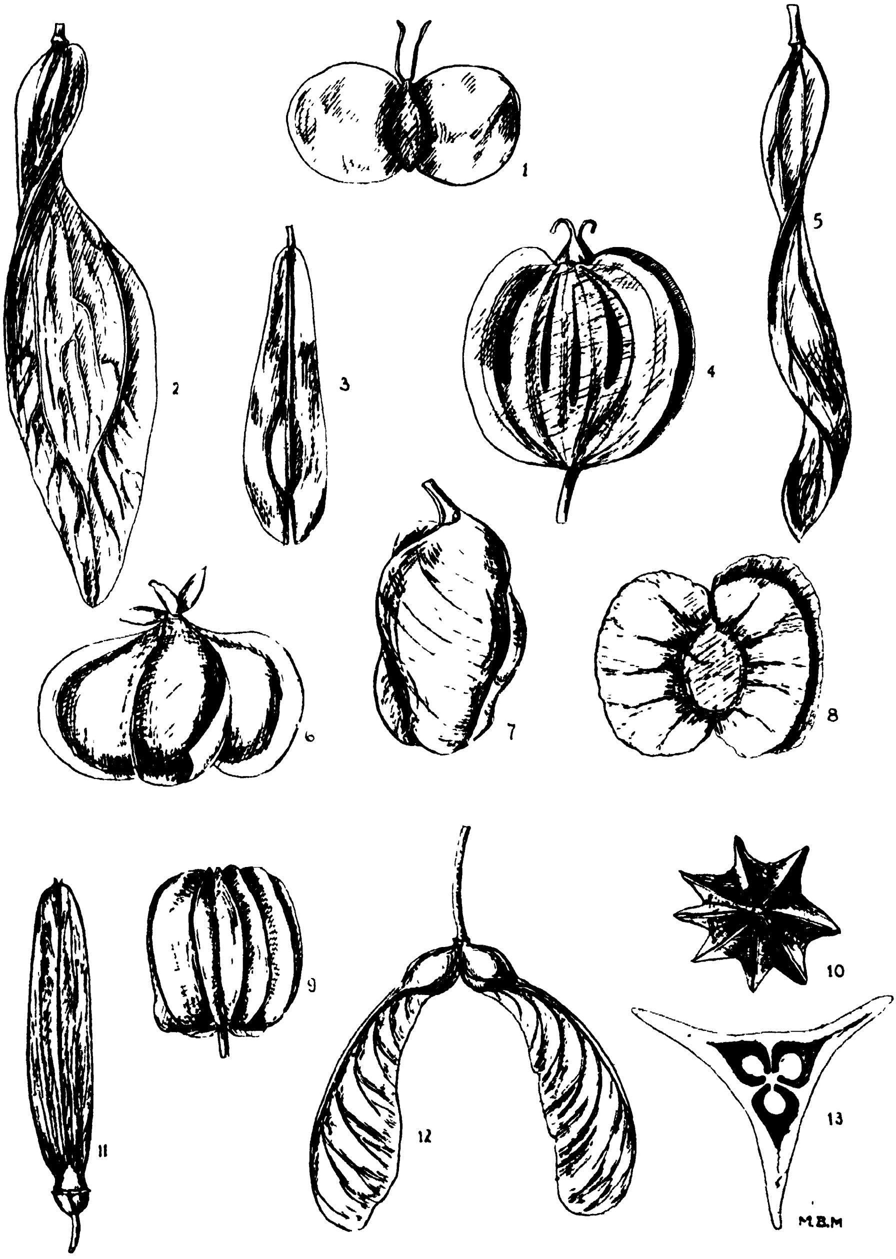
P. macrophyllus and *P. acuta* have 10 short, nearly equal, wings. *P. Curtisii* and *P. eximia* have similar wings. These are natives of the Malay Peninsula. *P. oligolepis*, of Borneo, and *P. polyantha*, of Java, have 5 wings. *P. burmanica*, Burma, has the largest and lightest fruit, with 4 large thin wings 1½ inch long and as wide. *P. triptera* has only 3 wings 1 inch long and ½ inch wide. This species is the commonest in the Malay Peninsula, and attains the height of 100 feet and more, and it is interesting to note that the species with the fewest wings is the most widely spread and abundant, for this species occurs all over the forests of the Peninsula, from Singapore to Perak, while the other species are much more local. Further research, however, may show some of them to be more widely spread, for these gigantic trees are very difficult to procure specimens from on account of their great height (Pl. IV, figs. 9 and 10).

The ovary in these plants is 5-celled with 2 ovules in each cell. In *P. triptera* the ovary is 3-winged, but in the species in which the fruit has more than 5 wings the ovary has as many ribs on it as it has wings, except in the case of *P. eximia*, which has 10 styles separate from each other, and each cell has an extra (false) septum, so that the 5 cells are divided into 10. However, it has but 8 wings in the fruit. *P. macrophylla* has a 5-lobed ovary and 10 wings on the fruit, and in *P. acuta*, in which the fruit has also 10 wings, the ovary is hardly lobed at all.

The extra wings appear to originate from ribs on the outer surface of the carpels. In all cases the fruit is one-celled and one-seeded, the remaining ovary cells and ovules aborting.

Carpodiptera africana, a large tree growing on sandy hills in Africa and

PLATE IV.



WIND-DISPERSAL. WINGED FRUITS.

FIG. 1.—*Betula alba* (fruit-enlarged).
,, 2.—*Koompassia malaccensis*.
,, 3.—*Isatis tinctoria* (enlarged).
,, 4.—*Heracleum Sphondylium*.
,, 5.—*Koompassia malaccensis* (samara, side view).
,, 6.—*Cardiospermum Halicacabum*.

FIG. 7.—*Sutherlandia frutescens*.
,, 8.—*Dodonaea viscosa*.
,, 9.—*Pentace eximia*.
,, 10.— ,, ,, (end view).
,, 11.—*Ventilago oblongifolia*.
,, 12.—*Acer pseudo-platanus*.
,, 13.—*Dodonaea viscosa* (in section).

[*To face p.* 76.

belonging to the same order, has a 2-carpelled fruit, each carpel having 2 wings. The whole 4-winged fruit is 2½ inches wide.

Columbia, also one of the *Tiliaceae*, is a tropical Asiatic genus of about 20 species of small trees or shrubs, 30 to 40 feet tall or less, growing in open sandy country. *C. auriculata*, of Siam and Cambodia, is a large bush. It has heavy round fruits with 5 very low wings ⅛ inch wide, hardly effective for flying, but they may serve to raise them above the soil and so allow them to be blown along the ground in the same way that *Halesia* fruits can progress. *C. evecta*, of Cochin China, and *C. subobovata* and *C. Teysmanni* have smaller fruits and wider wings. *C. serratifolia* and *C. scabra* have 3 or 4 wings on the fruit, which is altogether much smaller and lighter. In these the 4th wing is much reduced or often quite absent. The former is the most widely dispersed of the species, ranging from the Malay Peninsula to the Philippines. It is a small tree about 30 feet tall. Usually most of the other species have 4-winged fruits, but *C. javanica*, ranging from Java to the Philippines, and *C. diptera*, from the limestone rocks and open country of Perlis, have only 2 wings to the fruit, and no trace of any others. In these plants the fruit usually breaks up on the tree into from 3 to 5 cocci, each bearing 1 seed, so that each wing flies away carrying a single seed with it.

The genus *Gouania* (*Rhamnaceae*) is one of rather slender woody climbers, generally to be found on the edge of forests or scrambling over bushes and trees in open places. There are about 30 species, occurring in South America, Africa and Indo-Malaya. In all but 4 species the fruit is 3-winged, and breaks up on the raceme into 3 winged dehiscent cocci, each carrying 1 seed, much as in *Columbia*, though the fruit is much smaller. In one species, *G. bialata*, of the Sandwich Islands, one wing and seed are suppressed, so that the fruit is only 2-winged, and in 2 Madagascar and 1 Brazilian species the wings are not developed at all; apparently the fruit merely breaks up and the seeds fall out and roll away, as happens in the allied genus *Helinus*.

It is interesting to note how wide an area is covered by the wing-fruited species as compared with the scanty dissemination of the unwinged species, and the two or three species of the allied apterous *Helinus* of Africa and India, and there is no doubt that the abundance of the winged species all over the tropics is due to their powers of flight.

One-Winged Fruits (Samara).

The *Samara* is a thinly flattened one-seeded dry fruit, the pericarp of which is drawn out into a wing at one end, or in which the wing completely surrounds the seed (Round Samara). This fruit is indehiscent with a few exceptions. Occasionally, as in the Maples and Sycamores and some *Malpighiaceae*, etc., each separate carpel is winged and contains a seed, but when ripe they become detached from each other and float away independently and separately. After falling to the ground some yards away from the tree, they are blown further along the ground by wind until they have travelled often as far as 80 or 100 yards. This form of plant is very characteristic of big or medium-sized trees and lofty woody climbers (Lianes), in many of which the foliage is so dense that fruits unprovided with some such method of dissemination as this would in their fall either become entangled in the great mass of leaves and twigs, so that they would not reach the ground, or they would fall too near the mother-plant, and under the dense shadow formed by the mass of foliage would have very little chance of ever developing into an adult plant.

A number of herbaceous plants of large size, such as the Woad (*Isatis tinctoria*) and thick climbing herbs, such as some of the *Polygonums*, also

possess 1-seeded winged fruits which are similarly dispersed, and in some genera there are to be found all stages between the 3- or 4-angled fruits and fully developed winged fruits. There is also a tendency for a reduction of the number of wings from 3 to 4 in such multicarpellary fruits as develop wings, one to each carpel to a single wing, or when the carpels are not connate into one mass they separate from each other, so that each has but one wing.

It has been mentioned that if the carpels contain more than one ovule each, which is generally the case, only one develops into a seed, by which means a surer method of disseminating the plant is obtained than if more than one seed developed in the samara.

Frequently, when the seed is developed from one of the central ovules in the pod, it is thinner and more flattened than usual, which makes the whole fruit lighter, so that a samara with a central seed drifts horizontally, usually rotating round its long axis. If, on the other hand, one of the two end ovules develops into a seed, it remains more or less rounded, and the winged portion of the pericarp is formed of the upper or lower end, and is usually more or less lateral or inaequilateral. This gives the necessary spin to the fruit so that it falls vertically, rotating rapidly as it does so. The weight of the seed at the end causes it to fall in a vertical direction, while the inaequilateral wing causes it to rotate as it does so, and so retards its progress towards the ground, and the action of the wind on it during its slow fall causes it to drift a considerable distance from the tree.

It is immaterial for dissemination whether or not the basal or terminal ovule develops into a seed, for when it falls the fruit turns over in the air with its heaviest part—that is, the seed-bearing part—downwards. The evolution of the upper part of the pericarp into a wing, with only the lowest seed developed, is, however, the most common form of samara.

In cases like those of *Ventilago*, where the wing is straight from the top of the seed and not one-sided, or in *Koompassia*, where the thin leaf-like oblong samara has a central seed, it is a very common thing to find that at the base of the wing above the seed (or in *Koompassia* at the base of the samara) there is a half twist of the wing. When the fruit falls, this imparts a screw action to it which causes it to rotate rapidly, which it would not do if the wing were perfectly straight, and so further delays its fall.

Forms of Samaras.—Defining samaras as dry, flat or winged non-dehiscent fruits in which the flying organ is an evolution of part of the carpels or ovary, we can for convenience class them as SIMPLE samaras with no conspicuous wing, the whole fruit being flattened and thin, as in the *Acacias* and the *Crucifers*, *Thlaspi*, *Lunaria*, etc., and those in which the carpellary edge is prolonged into a wing on each side, as in the Birch, or on one side, as in *Casuarina*. Where the wing is distinctly evolved and lateral, as in *Acer*, or terminal, with the seed at the base, we can class them as BASAL samaras in order to contrast them with those in which the base of the fruit forms the wing, the seed being at the apex, or REVERSED samaras. Where the whole fruit is rounded and flat, the functional wing being circular and surrounding the single central seed, the ROUND samara, in which the fruit may be oblong with central seed, *Isatis*, *Fraxinus*. In fact, we get a large variety of forms of winged or flying fruits in which the whole carpel, or an accrescent edge, is thinned out so as to allow the fruit to be dispersed by the wind.

Evolution of the Samara.—The fruit of the *Leguminosae* is typically an unicarpellary pod containing a number of seeds. When ripe it dehisces both at the suture of the carpellary leaf and along the midribs, or along the sutural edge only. This is often done explosively and so suddenly that the seed is ejected to a short distance (*see* Explosive Fruits, p. 663).

In the Laburnum (*Cytisus Laburnum*) the pod, which contains several rounded

seeds, dehisces in this manner, and the seeds are ejected by the explosion, but occasionally it happens that one or two seeds remain attached to one of the valves, the funicle not breaking away. Eventually the valve to which they are attached becomes detached from the tree and is blown away, bearing the seeds with it, and on reaching the ground may still be blown along by the wind, being assisted by the valve acting as a sail. I have seen seeds thus carried for 70 yards from the tree, a greater distance than if they had been merely explosively ejected. As seeds dispersed in this manner benefit by the further distance they travel from the parent tree, it is easy to see how in course of time a variety or species might be evolved in which this method of dispersal was always the case.

Albizzia moluccana is a lofty tree about 80 to 100 feet tall, with a smooth bare stem with a large spreading crown (coma). The pods, which are about 4½ inches long and ½ inch wide, are very thin and light, and dehisce normally into the 2 valves. The seeds adhere firmly to the valves, and are borne by the wind to a considerable distance from the tree, very much further than the mere explosion would carry them if they were as easily detached from the placenta as, for instance, in the Gorse. Unfortunately I have not kept a record of the distance to which they can fly, but as the tree usually grows in more or less open localities, the valves not only flutter in the wind as they fall some distance from the tree, but may be blown along the ground still further. As the tree is very prolific and grows with great rapidity in open spots and thin woods, it spreads very fast, but seems to make less progress where the forest is dense. It is not a native of the Malay Peninsula, although I have found many of these trees in long-abandoned coffee plantations now overgrown with high forest, but they had spread no further. In one spot where the forest had been felled, and only secondary scrub later covered the ground, it spread with some rapidity over a considerable area, a great many trees coming up in a few years. Here it should be noticed how small a modification is required to produce a wider and more rapid dispersal of a tree than it would otherwise obtain. In the pods, of which the seeds are dispersed only by the explosion of the carpel, it is essential that the funicle which attaches the seeds to the wall of the carpel should be easily broken, so that the seed is instantaneously ejected. In the Laburnum we find occasional fruits in which the funicle is tougher and so retains some of the seeds. These seeds by this very slight modification are carried further than those with a more fragile funicle. In the *Albizzia* the funicle is normally tougher, and continues to hold all the seed firmly attached to the light valve. After dehiscence, aided by this modification, the tree is much more widely disseminated. In the first place it flies further directly from the tree, and in the second place, when it alights it can be blown still further along the ground, if open, by the continuing wind blasts. In this mode of progression in most plants of this character the seeds attached to the wing (the valve of the pod) are knocked off or fall off gradually as it is blown along the ground, so that they are scattered separately in the course of its flight.

Robinia pseudacacia is a well-known American Leguminous tree very freely cultivated in our gardens and parks. It attains a height of 50 to 80 feet, and bears numerous white flowers, which produce an abundance of light linear pods 3 inches long and ½ inch wide, containing from 2 to 11 small, flattened oblong seeds ¼ inch long. The fruit does not dehisce on the tree, but remains hanging down from the branchlets until after the leaves have fallen, and in the late autumn they become detached from the pedicels and fall to the ground. Most of them fall before the end of the year, but some remain hanging to the branches until March or April. I have seen a few of these late ones dehisced on the tree. Very soon after reaching the ground the pods dehisce and separate

into the 2 thin valves, each retaining some of the seeds attached to the placenta by short funicles. Usually a number of the seeds are abortive, and 2 or 3 only may be fully developed. The pods, being very light, are blown to some distance from the tree before they reach the ground, usually about a dozen yards or so. After the dehiscence the valves are blown along the ground to a considerable distance, 100 yards or more.

Asa Gray says that in America the pods do not fall till the end of winter or beginning of spring, but in England they fall as above described. As they travel the seeds are gradually shed, and so are widely scattered. I have seen valves carrying 1 or 2 seeds, after the winter storms, lying at a distance of 150 yards from the tree in April, but most of the seeds are shed before the end of the year. I have every reason to believe that they frequently travel much further than this on smooth open ground, pathways or roads. On grass plots I find that the thin valves are very attractive to earthworms, which pull them down into their burrows, probably in order to plug them as they do with dead leaves and sticks. In so doing they must actually plant the seed in the soil below the surface.

Compared with the Laburnum, the method here adopted is a great improvement. The pod does not dehisce on the tree, so that no seed is wasted by falling on the ground beneath it. The seed is not detached from the funicle till the pod has separated into its two valves, and often remains attached, in spite of wind and rain, for as long as 6 months, allowing of its travelling to a much greater distance than does the pod-valve of the Laburnum.

In some of the other *Albizzias* we find a further modification. In *A. pedicellata* we find that the pod does not dehisce at all. It becomes thin and papery, the seeds, which are thinner, flatter and lighter in proportion to their size, are reduced in number, so that the pod, readily detached from the tree, drifts to some distance from it before it alights, and, being not much heavier than many leaves, is blown along the ground, carried by puffs of wind. In this case the pod is not only lighter, but much broader than in *A. moluccana*, so that it exposes a greater surface to the wind and thus it flies further, just as the broad light leaves of the plane tree are drifted along the ground further than those of smaller and heavier-leaved trees.

The pod of *Albizzia pedicellata*, when ripe, becomes not only thin and light, but brittle and almost corky. It contains from 2 to 3 seeds, and is from 8 to 12 inches long and 2 inches wide, and as it travels over the ground it breaks up quite irregularly into pieces, each containing a single flat thin seed. These again may be blown further along, and so it becomes further scattered, but in any case the whole pod as it moves breaks off the seed-bearing portions against the ground until all the seeds are scattered about.

Calpurnia aurea, an African tree 10 to 15 feet tall, has a thin papery pod containing 7 seeds, much resembling that of *Albizzia pedicellata*, but many pods are short and contain only 1 seed. *Cladrastis*, trees of China, Siberia, and North America, have also typically several-seeded pods, but in most species 1-seeded ones occur, and *C. platycarpa* has always a 1-seeded pod. This reduction of from several seeds in a pod to one, leads naturally to the orbicular winged 1-seeded pod, the round samara, such as the fruit of *Pterocarpus*.

It is obviously an advantage to the tree to possess single-seeded pods in such as are dispersed by flight, inasmuch as, though actually fewer seeds are produced than by a tree with many-seeded fruit, the seeds are more widely separated from each other, and thus have a better chance of developing into trees than if 2 or 3 seeds sprang up close to each other.

The reduction of the many-seeded to the 1-seeded pod leads again to a form in which the pericarp becomes tougher and more corky for the purpose of sea-dispersal. In these cases the tree or climber grows on the shores, and

the samara is blown into the sea. It is then borne by currents frequently to long distances, to be at length thrown up by the waves on the shore, where it probably germinates and grows. An account of these appears under the chapter on sea-dispersed seeds (*see* p. 276), but it may be of interest here to note that though these plants are clearly descended from species with many-seeded pods, and consequently of later evolution, they are far more widely dispersed throughout the world than their ancestors, with many-seeded pods.

Leguminosae.—Among these we have the genus *Ateleia* occurring on the shores of the West Indies, and *Derris uliginosa*, the most widely dispersed of its large genus, occurring on the sea coasts all over tropical Asia. In the genus *Derris*, woody climbers or small trees, natives of tropical Asia, with out-liers in Australia, Africa and South America, the ovaries contain from 2 to many ovules, but most of the ovules abort and very frequently only 1 develops into a round or elliptic thin flat seed.

Derris thyrsiflora, of the Malay Peninsula, is a woody climber on the edges of jungle, or frequently a large sarmentose shrub in open country. Its great panicles of innumerable white flowers produce comparatively few fruit. The ovary contains 4 ovules, of which only a central one develops into a flat seed enclosed in a thin papery samara 3½ inches long and 1 inch or more wide. When detached it flutters down from the plant and, having fallen, drifts along the open ground in the wind till it is checked by some obstacle. In the allied *Derris sinuata*, a scandent shrub inhabiting tidal mud, the ovary contains 5 to 7 ovules, of which 1 to 4 develop into seeds. As dispersal by wind would be useless to a plant growing over tidal rivers, the pod is not thin and papery, but rather thick and firm. At the points where the ovules are aborted the pod is indented on the edges of both sides, so that it breaks into joints, each containing a seed. The joints do not dehisce, so that the seed is borne away by the tide enclosed in its portion of the pod. It is a far more distantly distributed plant than *D. thyrsiflora*, being widely spread from Ceylon to the Malay Peninsula and islands.

In *D. thyrsiflora* and some species, only the central seed is developed. In other species, and in allied genera, we find either the terminal or basal seed developed only. In *D. robusta*, of India, in some fruits it is the basal ovule which develops into a seed, while in others it is the terminal ovule which develops, the empty part of the pod becoming thin and light and forming the wing. The first form, with the seed at the base, may be called the TYPICAL samara, and the one with the seed at the tip the REVERSED samara. The typical samara is the most common form of this kind of winged fruit, and is characteristic of the Maples, *Acer* (*Aceraceae*). The reversed samara is less common, but occurs in many of the South American trees, such as *Myrospermum* and *Myroxylon*. The reversed samara appears to fly as far as the typical samara, for as all these fruits, when detached, fall with the heaviest part downwards, the reversed samara turns over in the air as it falls and adopts the same position as the typical samara, e.g., *Pterolobium* of the Malay regions. Many of these winged fruits are heavy, and consequently when they reach the ground cannot continue their flight along it. These are, however, usually lofty trees of dense jungle, where no drifting by wind along the ground would be possible. The wing has finished its work when the fruit reaches the ground.

There is a slight modification of the leaf-like samara, with a single central thin seed, which occasionally occurs and which has very important results. It consists in a small twist of the fruit at the base close to the pedicel, by which, as the fruit falls through the air, a screw action is produced, and the thin fruit rotates horizontally as it flies. This action not only keeps the fruit longer in the air and allows a breeze to carry it further, but also actually propels it further away from the tree. It is well seen in the gigantic Leguminous trees

Koompassia, of which there are 2 species occurring in the Malay Peninsula and Borneo. They usually inhabit the jungle forest, overtopping most of it by their great height, 150 feet or more, and are often seen in more open country where the forest has been cut, as, owing to the hardness of the timber, Malays are unwilling to attempt to fell them. *K. malaccensis* flowers and fruits in most years, but *K. parvifolius* about once only in 25 years (Pl. IV, figs. 2 and 5). The slow flight of this fruit, lying horizontally in the air and rapidly rotating, is most remarkable, and with a good wind I have seen it fly a distance of 61 yards from the tree, and there is little doubt, judging from the young trees which have certainly been derived from it, that it often flies a much greater distance.

A somewhat similar case is that of *Ailanthus* (*Simarubaceae*), of which there are a number of species, mostly lofty trees, natives of the warm parts of Asia. In *A. imberbiflora*, of Australia, the base of the samara is twisted, as in the *Koompassia*, while in some of the species, e.g., *A. excelsa*, of India, *A. grandis* and *A. glandulosa*, the tip of the samara is even more conspicuously twisted. The samaras of the Ash, *Fraxinus excelsa* (*Oleaceae*), popularly known as Ash-keys, are slightly bent or twisted just above the seed sufficiently to produce the horizontal rotatory screw action as the fruit falls from the tree. The samara in this case consists of 2 carpels firmly joined together, in which a single seed is developed.

The fruits, when falling from a tree of about 20 feet tall in a light wind, fly about 14 yards before reaching the ground, and in one case where this tree stood in an open field 2 seedlings from it were found growing a distance of 135 yards away. The samaras had doubtless been blown along the meadow to a shrubbery where they could grow without injury from cattle or grass cutting. As the Ash attains a height sometimes of 100 feet, it is probable that the samaras of such a tree fly much further than they did in this small 20-foot tree.

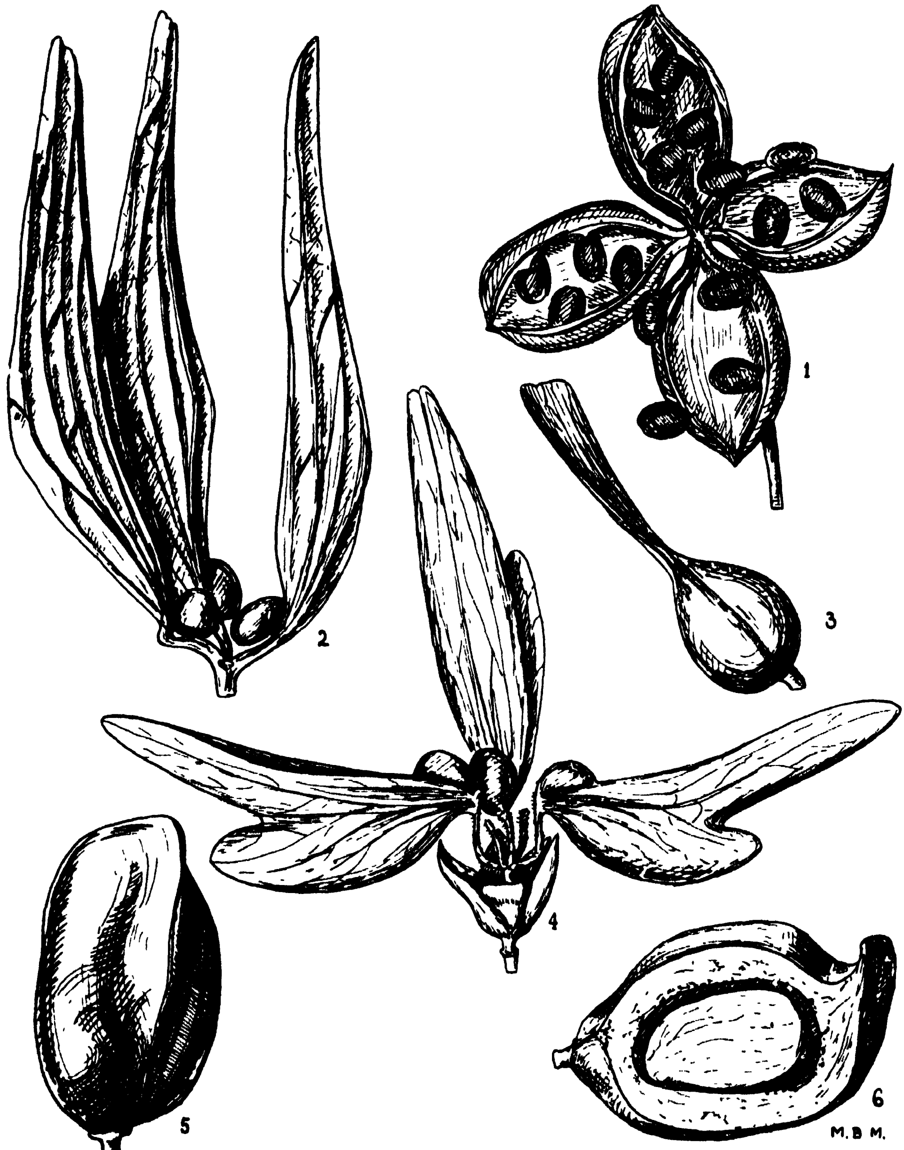
In *F. coriacea*, of North America, and *F. ornus*, the Manna Ash of Southern Europe, the samaras are not twisted, but flat. They fall straight from the tree. In the Manna Ash they are oblong, blunt, narrowed slightly at the base, 1½ inch long and ¼ inch across in the widest part. They fly from the tree in a fairly strong breeze about 12 yards, but apparently not so far as in the common Ash, as they have no screw action.

Another form of producing the screw action in Leguminous pods lies in the tip of the fruit being unequal-sided and one point of the tip overlapping the other so as to form a slightly raised wing, as in the big West African tree *Amphimas ferruginea*. From herbarium specimens of this it is concluded that the pod actually dehisces on the trees, and that one valve carries the single oblong flattened seed.

In some of these thin 1-seeded flat pods the upper end is slightly twisted, so that the screw action is effected from the apex. *Peltophorum*, a widely distributed genus of usually comparatively small trees, has this arrangement. Species occur in Africa, the Malay Peninsula and islands, and tropical America. *P. ferruginea* and *P. dasyrachis*, in the Malay Peninsula, are spreading trees 20 to 40 feet tall, growing in open country. They are widely spread all over the Malay region to Australia, one occurring in Earl Grey's Island. The seeds are from 1 to 4 in a pod, but usually 1 only. A similar screw action modification is to be seen in *Smythea macrocarpa* (*Rhamnaceae*), a climber in the Malay Peninsula. In this and in *S. lancifolia* the base of the oblong winged fruit is twisted, so that in falling the fruit rotates vertically. In *Ventilago oblongifolia*, an allied plant, the two sides of the terminal wing at the base just above the fruit are incurved so as to give a similar action when falling (Pl. IV, fig 11).

The seeds in the flat thin pods are generally thin and flat also, but in

PLATE V.



EVOLUTION OF FRUIT FROM BIRD-DISPERSED TO SEA-DISPERSED.

FIG. 1.—*Sterculia laevis* (reduced).
" 2.—*Scaphium Wallichii* (reduced).
" 3.—*Tarrietia Curtisii* (reduced).
" 4.—*Pterocymbium campanulatum*.
" 5.—*Heritiera littoralis*.
" 6.— " " (in section).

[*To face p.* 83.

Myrocarpus frondosus, a South American tree, the pod of which is lanceolate-linear and 2½ inches long and ½ inch wide, the central seed is very narrow and cylindric, much like that of the Ash. The broader, flat, leaf-like leguminous pod with a central seed, which flutters to the ground and may be blown further along by the wind, usually has a rounded or oblong thin seed. Plants which have such pods are characteristic of open country or of forests bordering on open country, such plants as *Derris thyrsiflora*, *D. scandens* and *Mezoneuron*, being all climbers in the Malay region.

A very striking and interesting evolution of the wing is given by the trees of the section *Sterculiaceae*. In the genus *Sterculia* the fruit consists of 5 free carpels, coriaceous and spreading, when ripe, in the shape of a star, of a magnificent scarlet or bright rose colour, splitting along the inner edge. The deep blue-black seeds hang from the edges of the opened leaf-like carpel, and are much sought after by birds. These trees or shrubs usually occur in open country or in woods, where fruit-eating birds are plentiful, but there are a number of allied genera which occur in the dense forests where birds are scarce, and are often vast trees, and these have the fruiting carpels developed into plain-coloured winged organs (Pl. V, fig. 1).

Scaphium comprises a small number of often gigantic trees inhabiting the forests of Burma, Siam, the Malay Peninsula and Borneo. The carpels, reduced to 3 or 1, are thin, green leaf-like boats from 6 to 8 inches long, at the base or stern of which is a single seed. They are broadest at the base, above which they become gibbous below and gradually taper to the upcurved tip (Pl. V, fig. 2). The sides of the boat are quite thin and light green in colour. The trees fruit at a height of 60 feet or more. The boat-shaped carpels when detached, as they are, singly, drift along in the breeze, the gibbous underside causing them to rotate briskly as they float along. In thick forest I found that the fruits from a tree 30 feet tall flew to a distance of 50 yards. From more lofty trees, with a strong gale blowing, they would probably go very much farther. The seeds are remarkable for possessing in the testa a mucilage containing bassorin, which, on being wetted, exudes to a great extent and forms a slimy mass. Whether this serves any purpose in repelling rats which might eat the seed, or plays some part in causing the seed to adhere to the soil, I do not know. Schomburgk mentions that he came across a spot in Siam where the mucilage of the fallen seeds was so abundant that his horse was unable to cross the slippery surface.

Pterocymbium is also a large tree, 60 feet or more tall, inhabiting dense jungle, like *Scaphium*. The carpels resemble those of the latter, but 5 or 6 remain. These are dark purple and much smaller, being only 3 or 4 inches long and with the gibbous portion prolonged into a distant rounded lobe, the rest of the carpel being a linear, rather narrowed lobe. This prolonged lower lobe of the boat probably serves to increase the rotation of the falling fruit and keep it longer in flight. There are 2 species, natives of Burma, the Nicobar Islands, Malay Peninsula and Java (Pl. V, fig 4).

Tarrietia.—These are Malayan trees of vast size, often 150 to 180 feet tall, occurring in dense jungle. In these the large seed is enclosed in a rounded carpel terminated by a longer or shorter curved spathulate wing, stiff and coriaceous, being clearly the upper end or prow of the boat of *Scaphium*, the basal part of the boat being closed over the seed and much thickened. The fruit is a heavy one, which is often the case in these gigantic trees, and this helps it to crash through the dense foliage below. The wing is sufficiently developed to give the fruit the rotary motion necessary to carry it away from the tree (Pl. V, fig. 3).

In the allied *Heritiera* the wing is much reduced in the forest species, so that it is nearly functionless. In *H. elata* it is only ½ inch long, while the rest

of the fruit is three times as long. (In *Tarrietia perakensis* the fruit is 1¼ inch long and the wing 2 inches long.) The tree is over 100 feet tall. A big tree of this *Heritiera* in the Singapore Garden jungle fruited heavily one year, and I observed a very large number of the fruits lying at the foot of the tree. Most of these germinated and a large crop of seedlings appeared, but as each year went by, fewer and fewer were seen to be alive, and only those throve which, partly by bounding when they fell or by rolling, reached some yards distant from the tree. *H. fomes*, of India, is shown by Troup to be largely distributed by river, the seeds floating in abundance in the spring tides (*see* Water Dispersal, p. 262).

Finally in this series of closely allied plants all found in the same area we get the seashore *Heritiera littoralis*, in which the wing has quite disappeared. The fruit is much bigger than in that of the forest *Heritiera*, having a thick, light corky pericarp. It is a maritime tree widely distributed in mangrove swamps and sea-beaches by the adaptation of its fruits for sea travel (Pl. V, figs. 5 and 6).

Here we have the story of the evolution of a fruit from one consisting of 5 free coloured follicles with black drupaceous seeds (bird-dispersed) through a single open follicle with one basal seed (*Scaphium*) adapted for wind-dispersal. The flying mechanism is reduced and the seed enclosed in the carpel (*Tarrietia*), and finally the wing disappears, the pericarp becomes light and corky, and we have the river-dispersed *Heritiera fomes* and the sea-dispersed *Heritiera littoralis*. The whole evolution has taken place in the Burma-Malayan region.

Berrya (*Tiliaceae*).—This genus of tropical Asiatic trees has a somewhat puzzling distribution, and its means of dispersal are not at all clear. The trees are of considerable size, and one of them, *B. ammonilla*, gives the valuable Trincomalee wood. The capsule is of 3 carpels, each furnished with 2 linear oblong wings about 1 inch long, and containing a number (1 to 4) of small angular seeds covered with stiff hairs. These carpels dehisce and release the seeds. The species are mostly allied and similar in fruit.

B. ammonilla is found in Ceylon (doubtfully wild in Southern India), Burma, Andamans, Lankawi Islands, Borneo, Java, Christmas Island, Philippines, Australia, Tahiti.

There are slight differences between the plants here classed as *B. ammonilla*. The Christmas Island and Australian plants have smaller fruits and flowers, but these may be only local strains. So far as I have seen, the tree does not grow on the seashore, though it grew not far off, on coral limestone rocks on Christmas Island. In Ceylon it grows inland in dry places. Its distribution given above is distinctly insular.

It is quite impossible that a winged capsule like this, or the separate winged carpels, could be drifted by wind to any great distance and yet retain the seeds. The wings would certainly serve to carry the whole fruit or the separate carpels some distance from the tree. I cannot say for certain whether the capsules dehisce on the tree or after falling. Observations on the living plant are required.

Guppy (" Notes of a Naturalist," p. 379) writes :—

> " The genera *Buttneria* of the *Sterculiaceae*, and *Berrya* of *Tiliaceae* are " represented (in Tahiti) by species which must owe their dispersal to birds, " though I have no data relating to their dispersal, their fruits being capsular."

This I think extremely improbable. There is nothing in the fruit or seed to attract birds, and it is hardly likely that any inland bird of Ceylon would carry the plant to sea-girt islands. It is much more likely that it is transported by sea. It peculiarly affects dry regions, which accounts for it being absent in

the *wild* state (it is sometimes planted in gardens) from the Malay Peninsula and such-like wet regions, and for its occurring in dry rocky spots in islands.

In the order *Rhamnaceae* the ovary is usually 3-celled, with 1 ovule in each cell, and the fruit (all ovules but 1 being suppressed) is usually a drupe. *Ventilago*, a genus of woody climbers over bushes and small trees, has, however, a winged fruit. It has a 2-celled ovary, but only 1 ovule develops into a seed. The small round pea-like dry fruit has a terminal erect linear oblong blunt wing about 2 inches long. The plants climb on bushes usually by river banks and in open woods, or borders of forest. They are about 50 or 60 feet long, and the species extend all over tropical Asia and also occur in Africa. Forming as they do a great mass of foliage tangled up with the bushes and trees of the open forest edge, these winged fruits are well adapted for spreading away from the thickets by means of the wind (Pl. IV, fig. 11).

In the Birches (*Betula*) (*Betulaceae*) the small fruits, about 2 to 2·5 mm. across, are usually winged, with a rounded wing on each side (Pl. IV, fig. 1). They are borne in a catkin of bracts which breaks up when the fruit is ripe. In the dwarf bushes *B. nana*, of the arctic regions, *B. Michauxii*, of North America, and *B. chinensis*, probably a shrub, the nutlets are hardly or not at all winged, and the breadth of the wings and corresponding small size of the nut varies very much in the trees and tall shrubs. In the common English Birch (*B. alba*) the nut is very small and narrow, and the wings large and rounded, the whole fruit being about $\frac{1}{8}$ inch across. As the long pendulous branches sway about when the catkins are ripe in November, the seeds fly to a considerable distance. I have traced them for 40 yards, but they probably go much further. They usually fall flat, and are blown along the ground. They float easily and, though hardly river-bank plants, may be readily dispersed along the rocky banks of streams in Scotland and elsewhere. They are certainly dispersed by rain-wash.

Robert Smith (in " A Paper on Seed Dispersal of *Pinus sylvestris* and *Betula alba*," Ann. Scot. Nat. Hist., 1900, 43) examined the north part of the moor of Fettersloch in Scotland, and, judging by the distance of the Birches on the moor from the wood, estimated the flight of the Birch fruits at 489 yards. It is quite likely they might go for this distance in a gale through the air, but they might have been carried along the ground by following blasts or rain-wash.

The Birches range from the arctic regions of Europe and North America through the whole of Europe to temperate Asia, North India, China, Japan and North America. They are absent from the Canaries and Azores.

The Alders (*Alnus*) have the same structure of fruit as the Birch, but the cones do not break up and release the seeds with the bracts; they merely open and let the seed fall out to be blown away. The seeds are rather thicker and more corky than those of the Birch, the wings usually shorter, and in *A. glutinosa* absent. Most of them at least inhabit the banks of rivers and swampy places, and are dispersed more by water than by wind. The wind serves to blow the seeds into the water, which, if moving as in a river, carries them away till they are stranded in a suitable spot for growth. Like the seeds of the Birch, they are produced in great abundance, and I have seen the end of the lake in Kew Gardens densely covered with millions of seeds blown into the water from about a dozen small trees on the banks, and driven along therein by the wind. The distribution of the Alders is wider than that of the Birch, but it is not (like that genus) arctic. Species are found in Europe to Persia and Syria, Siberia to Kamtschatka, China and India, North and Central America to the Peruvian Andes. They are absent from Africa, though Drege in 1839 found the European *Alnus glutinosa* at the Cape, where it must have been planted.

Casuarina (*Casuarinaceae*), the She-Oaks, are tall trees with long pendent

branches, on which hang small cones of female flowers, with a pair of bracteoles which increase in fruit and form two woody valves enclosing the small nut, which has a terminal wing. When ripe the valve-like bracteoles separate, and the nut is shaken out by the wind. As the branchlets are long and very slender, they sway about violently in the wind, and nuts are blown and thrown to a considerable distance. The trees are chiefly inhabitants of the Australian deserts, but there are 3 or 4 species which are found in the Malay Islands and Fiji. One of these, *C. equisetifolia*, ranges from Australia through the Malay Islands to the Mascarene Islands and East Africa, and also to the Polynesian Islands. It owes this wide distribution to sea transport, and is treated in this aspect under sea-dispersed plants (*see* p. 316). When the nuts have drifted to land and the plants have grown up, they are spread further by the action of the wind, and form a single line on the sandhills by the sea, or sometimes a small forest of scattered trees, spreading as far as the soil (pure sand) will let them. It seldom grows beyond the sand dunes, though it is nowadays with some success largely cultivated inland for timber. This is another case of extra wide dispersal of a wind-disseminated plant by its modification as a sea-traveller.

Basal-Seeded Samaras.—In the typical form of samara the seed is at the base of the fruit and the wing is above. In the *Leguminosae* the wing portion of the samara is merely the flattened and thinned upper part of the pod in which the seeds are aborted, but in most of the other cases the wing appears to be an out-growth of the pericarp of the carpel, which never contained ovules at all. As usual in this class of fruit, even if the ovary contained more than 1 ovule, only 1 ever comes to maturity. In cases where the fruit is large and heavy, as in big trees, it falls vertically, rotating by its wings in the wind, but in light fruits, e.g., *Acer*, it flies horizontally, spinning round and round, and thus goes to a greater distance. The seed-bearing portion strikes the ground first, and, when on grass, the fruit remains with the seed on the ground, and, the wing being uplifted, in the end may be blown further along.

The best-known example of the basal-seeded samara is that of the genus *Acer*, Maples and Sycamores, European and Asiatic and American trees formerly included under the order *Sapindaceae*, but now generally separated and known as an order *Aceraceae*. They are trees of no great height, and generally found in open woods in temperate regions. The ovary is bi-lobed and contains 2 ovules in each cell, only 1 of which develops into a seed. The fruit consists of 2 opposed samaras, the seed-bearing portions in opposition, with the wings, long and unilateral, spreading away from them. When ripe they become detached and hang from a thread-like columella, from which they are blown away by the wind and, rapidly rotating horizontally, flutter to some distance. They descend with the heaviest part, the seed-bearing portion, lowest. In short grass they frequently stick with the seed in contact with the ground and wing erect, a very convenient position for germination. Very often in open ground (especially in the case of the larger ones, like those of the Sycamore) they are blown further along the ground.

The Maple (*Acer campestre*) is much less abundant in England, and does not reproduce itself nearly as rapidly. The samaras are much smaller and are not produced in such abundance. It is a native of England, being known there from the Interglacial period.

The Sycamore (*Acer pseudoplatanus*) often attains the height of 60 to 70 feet, and has nearly the largest samaras of any species. The tree appears to have been introduced into England by 1551 (Turner), but for many years later it is only recorded as occurring in walks and places of pleasure of noblemen (Gerard's Herbal, 1595). It is now spread all over England, Scotland and Ireland, though no doubt planted intentionally in many places. It spreads

with remarkable rapidity, and seedlings appear everywhere within a hundred yards or so of a tree. Many of the seeds fall at the base of the tree, germinate, and soon perish; a smaller number are scattered in the direction in which the wind blows, to a distance of 40 yards or more, according to the height of the tree. One in my garden, 20 feet tall, shed its samaras to a distance of about 40 yards in almost a straight line, 2 or 3 yards apart. They are often blown further along the ground from the spot on which they fall, and, being frequently blown into rivers, are dispersed along the banks, developing into trees in spots suited for their growth (Pl. IV, fig. 12).

Acer platanoides, of Norway, has a slightly curved wing, somewhat of a boomerang shape. When it is blown off the tree it falls a very short way vertically, then, lying horizontally, it rotates with extreme rapidity, and in a stiff breeze will even ascend again in a boomerang way for a short distance. When it alights (unless supported by grass, when it stands up with the seed downwards), it lies flat on the ground and is readily blown along to a considerable distance by following gusts of wind. On reaching open damp soil, such as an open flower-bed, it remains still and goes no farther. From a tree 20 feet tall I observed a fruit fly directly in a very light wind to a distance of 30 yards; after heavier gales I found it had flown, probably partly along the ground, on a grass plot 100 yards, and as far along an asphalted path. A small tree, *A. dasycarpum*, about 20 feet tall, had small samaras which flew 39 yards in a light wind.

Of *Acer niveum*, of Java, Koorders states that the samaras weigh 100 milligrams, and that they can float for some days. The trees are large and widely dispersed in the Java mountains, where the wind is strong enough to transport them for about 40 kilometres (about 25 miles).

A large proportion of the *Malpighiaceae* have winged fruits. Most of the plants are woody climbers, but some are small trees and bushes. The larger number are South American, but there are some in Asia and Africa. The ovary is usually 3-, more rarely 2- or 4-celled, with 1 ovule in each cell.

In *Hiptage*, an Indo-Malayan genus, the 3 carpels are connate in fruit and possess but 1 seed. The carpels, 2 or 3, are indehiscent, and each bears 3 wings, 1 erect from the top of the carpel, which shows (in some species at least) a distinct central vein corresponding probably to the strong edge of the wing in *Acer*, while from the sides are 2 horizontal wings, both coriaceous. Thus there are 2 or 3 sets of wings to each fruit, making 6 or 9 wings in all.

The same principle holds in *Tristellateia*. It has a number of processes on the ovary which develop in the fruit into 6 or more linear wings. The majority of the species are natives of Madagascar and Africa, where they climb over low bushes and trees. *T. australasica* has the wings reduced to small processes of no value for flight. It is in effect adapted for dispersal by sea, and has a far wider range than any other species, viz., from the Malay Peninsula to Australia. It scrambles over bushes in tidal swamps.

In most of the *Malpighiaceae*, however, the carpels are simply winged like those of *Acer*, as in *Stigmaphyllum*, of South America, and *Rhyssopterys*, of Eastern Malay Archipelago, Australia, and Polynesia, and *Triopteris*, of Jamaica. They are all climbers, some species being quite low and slender twiners, like some species of *Stigmaphyllum*, which I have seen climbing over grass and low bushes like a Convolvulus, in Pernambuco.

In another set, like *Banisteria* and *Rhinopterix*, the wing is short and very broad, fan-shaped. In the latter—an African plant—the wing is unusually large, being 2 inches across. In *Banisteria* it is not so large, and the carpels are sometimes reduced to a single one. *Banisteria* is South American and African, and though some species have fan-winged fruits, others are like those of *Acer*.

Reversed Samaras.—In a winged fruit derived from a pod of several seeds of which only one comes to maturity, the fertile one may be either the basal one in the pod, a central one, or the terminal one. In the case of the two end ones the samaras fall vertically; in the samara with a central seed it drifts more or less horizontally. It is immaterial, so far as flight is concerned, whether the fertile seed is at the top or bottom of the pod, because when it falls the heaviest part, where the seed is, forms the base of the flying samara, i.e. it always falls seed downwards. It is most common to find the basal seed developed, but there are cases in which the terminal seed is the one which ripens. These I call " reversed " samaras.

One of the plants which produces this class of fruit is the gigantic liane *Spatholobus* (*Leguminosae*), of which there are a number of species inhabiting the Malay forests, where they climb to the top of the highest trees (Pl. VI, fig. 4). *S. ferrugineus* frequently climbs to a height of from 80 to 100 feet and more, and only flowers and fruits when it reaches to the top and gets full sunlight. There it produces large panicles of small flowers and an abundance of fruit. The fruits are narrow oblong samaras, 3 to 5 inches long and about ¾ inch across the wing, very thin, coriaceous and pubescent, bearing a single rounded seed at the tip, being the only one of the two original ovules in the ovary to develop. The samaras when detached fall seed downwards and are drifted away by the wind. A big plant climbing to the top of a *Terminalia* tree 150 feet tall shed its very light fruits so that they drifted in a slight wind about 20 yards from the tree; but that they can fly much further was evidenced by the appearance of a young plant in the jungle 188 yards away from the tree, and evidently one of its offspring. Another climber with reversed samaras is *Serjania glabrata*, and its allies (*Sapindaceae*), a South American scandent shrub with trilocular ovaries, each cell containing 1 ovule near the apex. These develop in fruit into 3 samaras, with the seed at the tip and the upper part of the carpel forming a broad inaequilateral wing. They separate from each other at the base, first having a fine central axis (columella), and eventually, becoming detached, float away in the wind. The allied small tree, 20 feet tall, *Toulicia*, has similar fruit.

Round Samaras.—The round samara is more or less circular, the seed being in the centre surrounded by a thin or stiffly coriaceous circular or semi-circular wing or wings. The wings are outgrowths of the edge or edges of the carpel.

In the *Leguminosae* we have some examples, such as the fruits of the magnificent trees *Pterocarpus*, natives of Indo-Malaya. Here the fruit is round and flat, nearly 2 inches across, the seed-bearing portion 1 inch wide. A similar wing occurs surrounding the pod in the oblong samaras of various species of *Derris*. The wing of *Pterocarpus* fruit is developed sufficiently to carry it some way from the tree, and the pod dehisces partially on lying on the ground, so as to permit the seed to germinate. It is probable that this tree, which is common on rocky shores of the sea and by rivers, is to some extent dispersed by sea, as it also occurs in the Andamans (Pl. VI, fig. 8).

A good example of the round samara of 2 or 3 carpels is *Ptelea trifoliata* (*Rutaceae*), a small tree about 20 feet high which inhabits open woods, limestone cliffs and banks of creeks in North America. The 2 or 3 carpels contain at first 2 ovules, but only 1 of these comes to maturity. The seed-bearing portion of the fruit is small and light and ¼ inch across, and it is surrounded by a thin, circular green wing ¾ inch wide. A tree in Kew Gardens fruits usually heavily in November, and the fruits are blown by the wind to a distance of about 6 feet from the branches, and are then frequently blown along the ground to a much further distance, sometimes as much as 80 yards. In falling from the tree they float quite flat and horizontal in the air, not rotating as

they go. When blown along the ground by a stiff breeze, they frequently run along on the edge like a wheel for part of the way. They go furthest on a gravel walk, but drift for some considerable way on grass. Among bushes they do not appear to drift any distance along the ground after falling.

A certain number of fruits on the tree have a third wing, counting the halves of the circular wing as two, but I find by experiment that when blown these do not go as far as the ones minus this addition.

The kind of localities given above for the tree in its wild state, viz., open woods, limestone cliffs and river banks, seem to be eminently suitable for the ready dissemination of this tree. There are several species of *Ptelea* recorded from North America, all very similar except one, *P. aptera*, which has drupaceous pear-shaped fruit with a sharp keel on each edge. It is the evolution of these keels into thin wings meeting at the ends, accompanied by the reduction of the main part of the carpel and the seed, which transforms a primitive heavy drupaceous fruit into a thin light samara. Strictly speaking, these keels and the wings evolved from them are out-growths of the midrib of the carpellary leaf.

The *Ulmaceae* (the Elms), *Ulmus*, and the *Holopteleas*, of India and Indo-China and Africa, have similar winged fruit to those of *Ptelea*, but the ovary is but of 1 carpel. They are big trees, the Elms growing to about 80 feet, and *Holoptelea integrifolia*, of Indo-China, attaining the height of 120 feet.

An interesting form of winged fruit is that of *Rindera* (*Mattia*), tall herbs of the order *Boragineae*. The 4 nucules have broad orbicular thin wings surrounding them. The flowers are borne in small compact heads with very short pedicels. In the fruit, which is about 1 inch across, the pedicel develops to a length of 1½ inch, so as to expose the winged fruit to the wind. The plants are found in Southern Europe and North America to Afghanistan and Siberia. The genus is allied to *Paracarya*, which are generally smaller plants with small fruits, with spinous processes usually on the sides of the nucule and sometimes on the much narrower wing edge. Though winged, these small fruits have a much less developed wing than in *Rindera*. The *Paracaryas* occupy the same area as the latter genus, but do not go as far. In *Rindera graeca*, which has the typical fruits of the genus, I find that remains of the spiny processes still occur. In many of these *Boragineae* the nucules, which are not winged, are covered with adhesive processes, and these plants are dispersed by animals. In *Paracarya* they are shortly winged, but still retain the adhesive processes, so that they may be dispersed both ways. In *Rindera* the wings are very much enlarged, and the adhesive processes have disappeared in most species. Here, in fact, we have the transformation of a plant adapted for adhesion to animals' fur into one adapted only for wind-dispersal.

A very pretty round samara is that of *Aspidopterys concava* (*Malpighiaceae*), a climber in woods in Burma, the Malay Peninsula, and Borneo. The 3 carpels are round, as thin nearly as tissue-paper, and white, orbicular and 1 inch across. Most of the species of the genus, which are found in China, India and the Malay Islands, have thin carpels, but they are oblong blunt at both ends, with a central seed, less thin than in *A. concava* and brown in colour. We find a parallel to these in winged seeds where genera with oblong truncate wings with a central seed are allied to or pass into those in which the wing is circular, and these quite resembling the fruits of *Aspidopterys concava*.

In the order *Cruciferae* we have a large number of plants in which the bicarpellary capsule typically contains a number of seeds which are released by dehiscence, and are disseminated by rain-wash or by being blown to a short distance, as has been already explained. The pods, or siliques, as they used to be called, are cylindric and elongate, or in one section globose or ovoid. In this latter section we have a regular sequence from the rounded many-

seeded capsule dehiscing, the outer valves falling off and releasing the seeds, to an indehiscent thin single-seeded samara, which is dispersed by wind and, on coming to rest, decays, allowing the seed to germinate some distance from the mother-plant.

In *Camelina* we find a more or less globose dehiscent capsule containing numerous seeds in each cell. In *Capsella* it is flattened, obtriangular, containing about 24 seeds. *Teesdalia* has the edges of the carpels prolonged into a short wing, with only 2 seeds in each cell. In *Iberis* the capsule is rather more distinctly winged on the edges and on the top, and each cell contains only 1 seed. In all these the capsule is dehiscent, and it seems probable that the object of the flattening of the fruit, causing it to become wing-like, allows a freer play to the enlarged replum to throw the seeds further away when the wind strikes it.

In the next stage of evolution we find a number of plants in which the carpels are dilated, when ripe, into wide thin wings, usually forming a circular or nearly circular papery indehiscent fruit containing a few seeds or a single one, and, when ripe, become detached as a whole from the plant. In *Thlaspi arvense* (the Pennycress), abundant in cornfields in England, the very thin orbicular cordate fruit, from $\frac{3}{4}$ to 1 inch wide, each cell containing 2 to 4 seeds, is readily dispersed by wind over open country when this annual plant perishes in the late autumn. Woodruffe-Peacock records how this plant was introduced into Cadney in Lincolnshire in a crop of oats, and was scattered for a distance of over half a mile by a spring gale.

As in all, or nearly all, of this class of plant in which the seeds are anyway dispersed by wind, the pedicel lengthens very considerably during the development of the fruit, and usually stands out widely so as to expose the seeds, or flying samara, fully to the wind.

Some species of *Iberis*, *Lepidium campestre* (which I have found growing on the top of a wall where its fruit had been blown by the wind), *Clypeola Jonthlaspi*, *Peltaria alliacea*, *Alyssum calycinum*, some species of *Aethionema*, and the well-known " Honesty " (*Lunaria biennis*), all possess this class of fruit.

Lunaria is a tall herb 3 feet or more high, the round papery fruits containing from 1 to 4 seeds. The fruits do not dehisce till they are detached from the panicle and have lain on the ground for some time. After dehiscence the seeds often remain attached to the two valves bearing them, which may be blown further along.

Isatis tinctoria (the Woad).—This tall crucifer, about 5 feet high, has numerous narrow, thin oblong oblanceolate samaras, $\frac{3}{4}$ inch long and $\frac{1}{4}$ inch wide at the widest part. They do not dehisce, and contain only a single central seed. They do not appear to fly more than a few yards (Pl. IV, fig. 3).

In the case of the samaras above-mentioned the 2 carpels remain attached together when the fruit flies away from the plant, but in some genera the carpels separate, and, after hanging some time by the slender thread-like columella, are soon drifted apart by the wind, carrying the seed with them. This is the case in *Biscutella*, of which there are about 10 species in Europe and temperate Asia, and 2 in North America, inhabitants of pine woods and rocky mountain slopes (Pl. VI, fig. 6), and in the big *Megacarpaea* of Central Asia, China and India. *Biscutella californica* is remarkable for having the fruit edged with hairs, which probably add to its flight, but doubtless also serve to attach the fruit to the soil when it comes to rest. It is possible also that it is by this means attached to passing animals.

Zilla macroptera is a thorny, shrubby crucifer inhabiting the deserts of the Algerian Sahara. The fruit when young is angled and beaked. When ripe it develops a pair of rounded wings. Massart mentions this plant as having its fruits blown along the desert sands. The only other species, *Z. myagroides*,

is a native of the Egyptian deserts. In this the fruit is wingless, but larger, very light and rounder, globose and beaked. It appears to be simply blown, rolling along the sands, the beak—persistent in this species—serving to anchor it when it comes to rest in a damper spot (Pl. VI, figs. 2 and 3).

These wind-dispersed crucifers naturally are to be found in open country, steppes, sandy desert, and in pine woods or mountain-sides, where the wind sweeps strongly during their fruiting season.

It does not follow that a plant possessing a samaroid fruit has always as extensive an area of dispersal as those which have a dehiscent capsule and derive little or no advantage from the wind. Much of the spread of a plant depends on its adaptability to environment, to climate, soils, proportion of moisture, etc., and the area of suitable habitat and land connection. Furthermore, plants may be more widely distributed by human agency than by any natural force.

Thus *Thlaspi arvense* owes its extensive area of occupation more to its dissemination in the seed of cereal crops than to its wind flight, although it owes its abundance in its area mainly to the action of the wind.

The order *Umbelliferae* includes a large number of herbaceous plants, chiefly of temperate and sub-tropical regions, of which the fruit consists of a pair of round or oblong 1-seeded carpels (mericarps) attached to a slender columella. Each mericarp contains 1 seed, and is usually indehiscent, and often possesses on the outer side several ribs, which are sometimes elevated into wings, and the edges of the mericarps are frequently thickened or produced into wings. With the exception of a comparatively small number which are furnished with an adhesive apparatus, or are more or less succulent and probably dispersed by birds, the mericarps become separated from each other from the base upwards, and are blown away by the wind even if they have no special modification for this purpose. In most species the inflorescence is borne on a tall stalk; in *Ferula*, *Dorema* and *Heracleum*, sometimes attaining a height of 8 feet. When fruiting this stalk becomes bare of leaves, and frequently the basal leaves also have nearly or quite perished, so that the falling fruits do not get lost among the mass of foliage at the base, and the fruits in umbels, being quite exposed to the full strength of the wind, are blown clear of the plant. The whole stalk becomes dry and brittle, and, when tall, by the mere act of falling throws the mericarps to some distance. Even in *Chaerophyllum temulum*, etc., in which the mericarps are rather long, slender and rounded, they are blown off the plant very soon after becoming ripe, and in many of these shorter plants the stalk is slender and easily swayed about by the wind, thereby adding to the distance to which they can be thrown. In the river-bank *Oenanthe* the edges of the mericarps are wing-like, though often rather thick and corky, to act as floats, but are sufficiently light to enable them to be blown into the water 3 or 4 yards from the plant and be drifted away by the current. But in some species the edges of the mericarp are drawn out into thin rounded wings by which they can fly to a greater distance, and also can be often drifted along the ground. Such is *Ligusticum Fischeri*, of Siberia and Russia, which has 2 broad wings on the edges and 3 shorter ones on each outer face. *L. Thomsoni* and *L. marginatum* Clarke, of India, are similarly winged. *Peucedanum oreoselinum* and several other species occurring in open sandy pastures have small, round, flat mericarps with very well-developed wings, though in the marsh-frequenting *P. palustre* the mericarps are not winged, but possess thick ribs, and are probably dispersed by water. In Africa there is a series of species referred to this genus which, instead of being herbs, are shrubs or small trees up to 20 feet tall. Such are *P. Grantii*, *P. Petitianum* and *P. araliaceum*, from East Africa and Abyssinia. These have very wide wings, and the allied *P. fraxinifolium*, of Central Africa, has

obovate winged mericarps, broadest at the top and gradually narrowing to the base.

The temperate or sub-temperate deserts of Palestine, Persia and Afghanistan produce a number of species of *Ferula* and *Dorema*, stout plants 8 feet tall or more, which possess thin flat strongly-winged mericarps ½ inch long. Such are *Ferula communis*, *F. collina*, *F. Blanchei*, *F. galbaniflua*. In these plants the stout stem dries up before the fruit is ripe, so that they are fully exposed to every gust of wind, and, indeed, readily fly if merely blown with the breath. A similar arrangement occurs in *Heracleum* and *Archangelica*, in which the mericarps may often be seen swinging from the filamentous columella so as to be most fully exposed to the action of the wind.

Archangelica is an inhabitant of the arctic regions, a tall plant over 6 feet high, so that the long stems rise above the winter snow, and thus the fruits can be blown by the blizzards along the vast tracts of snow-covered country to a great distance.

In the case of other small fruits dispersed by wind the system is much the same. The numerous and widely distributed genus *Thalictrum* (*Ranunculaceae*) have usually very small achenes at first with a somewhat fleshy coat (uncoloured), afterwards becoming dry and moderately light. These are always borne erect on the branch tips. But in one species, *Th. aquilegifolium*, the achene is much larger than in most species, and the pericarp is thin and papery and 3-winged. When ripe the achenes become pendulous on very slender elongated pedicels. The plant is a tall one, some 4 feet or more in height, and inhabits the edges of woods, where the breezes could soon drift away the achenes. It is interesting to note that though the achenes are better provided with means of wind-dispersal than *Th. minus*, in which the achenes, though rather chaffy when dry, are not winged, the latter is far the most widely dispersed of all the species. *Th. minus*, however, appears to have more adaptability to varying conditions, growing in rocky or shingly spots by rivers, on sand dunes, and some of its forms in damp spots high up in mountains —another case in which adaptability to different classes of locality and different climate weighs more than improved methods of dissemination in the distribution of a species.

Bract Wings.

In a number of plants the fruits, always 1-seeded, are dispersed by the aid of the bracts, or by persistent, and usually accrescent, leaves below the flower. To act as flying organs the detachment of the fruit must be below these modified leaves.

In some plants, like Lime trees (*Tilia*), where the leaves are alternate, there is only 1 bract to the inflorescence, which is few-flowered. In others, such as *Enkleia* (*Thymeleaceae*), which has opposite leaves, a pair of bracts (modified leaves) forms the flight organ. In *Sphenodesma* and *Congea* (*Verbenaceae*) the flowers are in a compact head, surrounded with bracts in an involucre, which primarily serves to attract insects for fertilisation. There are as many of these bracts as there are flowers in the head, from 3 to 7, but usually only 1 flower sets seed. In *Bougainvillea* the bracts are bright red or pink in flower; in *Linostoma*, white or pale rose, but they become pale and papery when the fruit is ripe, and are detached, adhering to the fruit, so as to be blown away separately. Most of the bract-winged plants are climbing shrubs, a few are trees, and these mostly belong to the orders *Cupuliferae* and *Juglandeae*, and a few are herbs.

Linostoma (*Thymeleaceae*) is a small genus of twiggy shrubs and lofty forest climbers allied to the erect shrubs or small trees *Wikstroemia*, which have

drupaceous fruits dispersed by birds. In a species from Siam, L. *persimile*, the plant is an erect bush 6 feet tall. The terminal leaves on the shoot below the small clusters of flowers, are pale or white, apparently as an insect attraction, and only 1 rather large fleshy drupe is produced to each cluster. This is too heavy to be borne away by the bracts. In the Brazilian L. *caryophylloides*, and apparently also in L. *ovatum* of the same country, the fruit is also large and fleshy, and the bracts play no part in its dissemination. But it is otherwise with the forest climbers of the Asiatic jungles. L. *pauciflorum*, of the Malay Peninsula, is a woody climber, scrambling to the tops of trees from 60 to 100 feet high. Its pendulous terminal shoots bear thin leaves, usually of a cream colour, though I have seen them rose-pink. Between the terminal pair are 1 or 2 inconspicuous flowers. In the Indian L. *decandrum* there is an umbel of 5 or 6 flowers between the coloured terminal leaves. In both of these only 1 fruit develops, and it is small and easily drifted away by the aid of the wings formed by the persistent terminal pair of leaves. Here the reduction of the number of fruit produced on the spray, and the persistence of the terminal pair of leaves, has converted a bird-dispersed plant into a wind-dispersed one, and has allowed the plant to be successful in climbing to the top of the forest.

Enkleia is a genus very closely related to *Linostoma*, and indeed was formerly united to it. It is also a very lofty woody climber in dense forests, climbing to a height of from 80 to 100 feet in the Malay region and spreading out long branches over the trees above their summits. The leaves are stiffly coriaceous, elliptic to orbicular. At the ends of the branches are spreading panicles, 2 inches or more long, of flowers ¼ inch long, 5 of which terminate each branchlet of the panicle. Below them are a pair of very narrow, inconspicuous bracts ½ inch long and $\frac{1}{10}$ inch wide. In fruiting, all the flowers but one disappear, and that one is developed into a small, nearly globose nut ¼ inch long. The peduncle below the flowers, at first very short, lengthens to 2 inches, and the bracts grow to stiff coriaceous leaves 3 inches long and over 1 inch wide, like the typical leaves of the plant, but narrower (Pl. VI, fig. 13). When ripe the fruit on its peduncle, with the 2 bract leaves attached, separates from the plant and, rotating rapidly, drifts away in the wind across the forest to some distance, very much in the same way as the fruit of a Lime tree does. In this case the uppermost leaves in the panicles, the bracts, perform no function during the flowering season, as do those of *Linostoma*, though they may act as bud protectors earlier, as they are thickly pubescent, but develop later into the wings for the dispersal of the fruit.

The strong woody climbers *Bougainvillea* (*Nyctagineae*), natives of South America, are well known to all horticulturists on account of their splendid pink or red bracts. Of these there are 3 to each cluster of 3 small inconspicuous flowers, which are actually shorter than the bracts. The bracts are ovate, thin, about 1½ inch long, and to each is adnate a flower. When the fruit is ripe it is 1-seeded and enclosed in the perianth attached at the base to the large bract, which has now lost its colour altogether and become dry, papery and whitish. The bracts now separate and are carried off by the wind, each bearing with it its 1-seeded fruit. Here the bracts perform two functions —in the flowering time as attractions to insects to the inconspicuous flowers, and in the fruiting season as wings to disperse the seed, the colouring, being now useless, disappearing.

The section *Symphorema* of *Verbenaceae* includes 3 genera of climbing shrubs in which the small flowers are surrounded by an involucre, often red or white, of from 3 to 7 bracts. They occur on the edges of woods or in the open country, scrambling over trees and bushes, but never to any great height, usually about 20 or 30 feet.

Symphorema involucratum, of South India, has an involucre of 6 rather thin subspathulate leaves surrounding 6 or 7 flowers, of which only 1 or 2 fruit. The fruit is enclosed in an enlarged papery calyx, and only 1 seed out of the 4 ovules develops. In *S. polyandra* the bracts are quite spathulate, and the whole involucre is 3 inches across. Only 1 seed in the head ripens. *S. luzonicum*, of the Philippines, is similar, the flowers are pale blue and the bracts white.

Sphenodesme, a Malayan genus, is very similar to *Symphorema*, and has 6 or 7 lanceolate or spathulate bracts in a whorl enclosing as many small flowers, but only 1 or 2 produce fruits. *S. triflora* has only 3 flowers and as many bracts, which grow to a length of ¾ inch. They are purple, but small and inconspicuous in flower. Only 1 of the flowers is fertile.

Congea velutina has only 3 bracts, connate at the base into a cup, and 3 flowers. In all these, however, of the many flowers there are in the head, 1, or at most 2, rarely 3, produce fruit, and when the bract is coloured, the colour becomes faint or brown, and disappears as the fruit ripens (Pl. VI, fig. 15).

Neuropeltis (*Convolvulaceae*) is interesting, as the small capsule is subtended by 2 very broad rounded bracts, which, though small and inconspicuous in flower, develop into large wings forming a flat orbicular limb, when in fruit, 1½ inch wide (Pl. VI, fig. 10). The capsule, however, contains but 1 seed, the other ovules being aborted. It is a shrubby climber on the edge of forest in the Malayan region, a second species being Indian.

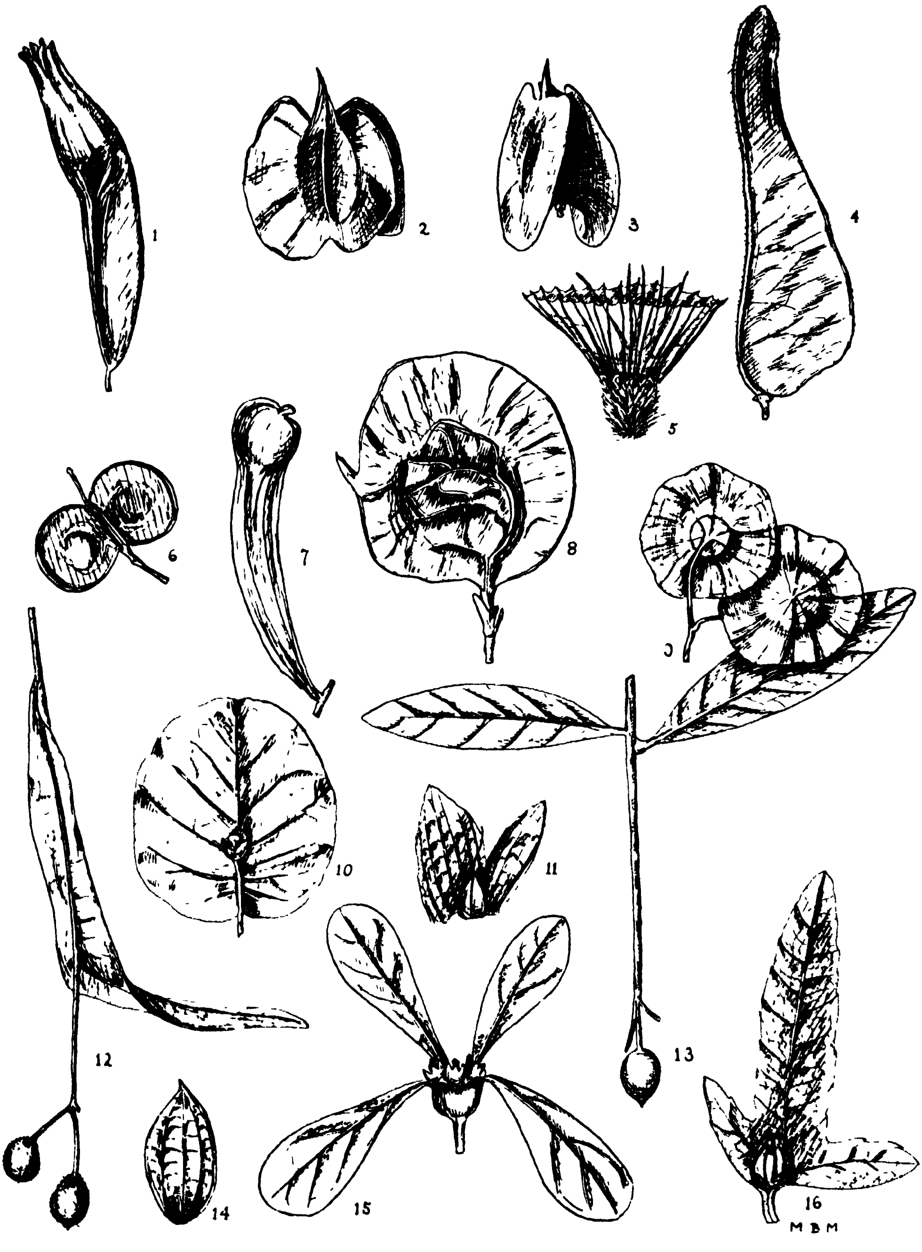
Dipelta (*Caprifoliaceae*) is a genus of shrubs allied to *Diervilla*, natives of China. The fruits are small and capsular. The ovary is 4-celled; 2 cells contain an ovule each; the others, sterile, contain several imperfect ovules, suggesting that the fruit was originally many-ovuled. Around the flower are 6 branchlets, 2 of which are deciduous early, 2 remain minute, and 2 develop into thin rounded ovate papery peltate wings, ¾ inch long and ½ inch wide, adnate to the base of the small ovary. They are inconspicuous and small in the flower, and add nothing in the way of attractiveness. The wings are so placed that the two edges meet behind the fruit, and the other sides spread so as to be exposed to the wind. Thrown into the air the fruits do not rotate, but when fallen, if the fruit lies on one wing, the wind acts on the other, which is erect like a sail, and the fruit can be blown rapidly along the ground. The shrub appears to be usually about 5 feet tall, so that the wind would not have much effect on the fruits during their fall, but they would be readily blown along by the wind when fallen. The plant grows in open spaces in woods, on cliffs, edges of forest and thickets. The allied genus *Abelia* has the sepals accrescent into wings by which the fruits fly. Some have reduced leaves at the base of the flower from which might be evolved the wings of *Dipelta*.

The Hop (*Humulus lupulus*) (*Urticaceae*) is a native of Europe, temperate Asia, China, and Japan. It was introduced into England about the year 1524, and has spread to a considerable extent in hedges and thickets. The female inflorescence has very small flowers subtended by a bract which, in fruit, enlarges to a blunt oblanceolate thin papery wing, which remains attached to the small nut. Though there are 2 flowers to a bract, apparently only 1 ever develops a fruit.

The cone of bracts eventually breaks up and the bracts are blown away by the wind to some distance from the climber. I have no record as to the actual distance to which the hop-bracts can be blown. They fly about 20 feet in my garden, but probably, when their path is clear, go much further.

In the Japanese Hop (*Humulus japonicus*) the bracts are never developed into wing-like organs, as in the common Hop, but remain attached to the nut, which is rather larger than that of the latter, and somewhat resembles that of the allied Hemp (*Cannabis*), as do the bracts. As might be expected,

PLATE VI.



WIND-DISPERSAL. WINGED FRUITS.

FIG. 1.—*Brunnichia cirrhosa*.
„ 2.—*Zilla macroptera* (front view, enlarged).
„ 3.— „ „ (side view).
„ 4.—*Spatholobus ferrugineus*
„ 5.—*Scabiosa stellata* (enlarged).
„ 6.—*Biscutella raphanifolia* (enlarged).
„ 7.—*Juliana astringens*.
„ 8.—*Pterocarpus indicus*.

FIG. 9.—*Paliurus aculeatus*.
„ 10.—*Neuropeltis racemosa*.
„ 11.—*Ostrya carpinifolia* (bract opened out).
„ 12.—*Tilia europaea*.
„ 13.—*Enkleia malaccensis*.
„ 14.—*Ostrya carpinifolia*.
„ 15.—*Congea velutina*.
„ 16.—*Carpinus betulus*.

[*To face p.* 94.

its area of distribution is very much more limited than is that of the common Hop.

The genus *Tilia* (*Tiliaceae*), the Lime trees, contains about 50 species of trees of no great size, usually from 30 to 60 feet tall, though exceptional specimens reaching a height of 100 feet are known to occur. They inhabit open woods or rocky and steep river banks in the north temperate region, Europe and America. The flying bract is narrow, oblong and blunt, much longer than broad, of a pale green colour, and is adnate by about half its length to the slender peduncle, which bears from 2 to 8 stalked flowers at the end. The bract does not appear to have any function during the flowering period, as it is but little more conspicuous than the foliage. Only from 1 to 3 of the flowers, as a rule, set fruit. These are small globose, usually hairy, 1-seeded drupes. When ripe the branchlet is detached below the bract and falls, rotating briskly, with the small fruits to some distance (about 30 yards) from the boughs. The weight of the fruit causes them to strike the ground first, and then the branchlet lies on the ground on the edge of the bract, which, acting as a sail, causes the whole to be carried further along the ground by puffs of wind. As the bract is blown along, the fruits are detached through their contact with the ground. Later the fruits may be carried along also by rain-wash. The distance to which the fruits are borne by the bract wing depends to some extent on the height of the tree and on the position of the inflorescence (Pl. VI, fig. 12).

Engelhardtia (*Juglandaceae*).—These are big trees of the forests of tropical Asia and South America. The leaves are pinnate. The bract in the female flower, which is very small, is 3-lobed, and fruit is, in most species, a small nut more or less enclosed in a cup with a long 3-lobed wing, as in the Hornbeam (*Carpinus betulus*). The trees are of great size, with pendent racemes of female flowers. Blume describes *E. spicata* as being from 100 to 200 feet, tall. I have not seen it more than about 80 feet high. *E. Wallichiana*, of Penang, is from 80 to 100 feet tall.

E. oreomunnea, of Costa Rica, is remarkable for the large size of its fruit. The central lobe of the bract is 4 inches long and ¾ inch wide, the shorter lateral ones spread at right angles to the other one, and all are rigidly coriaceous. In fruit the nut is covered with a shorter rounded lobe. The tree seems comparatively short, and is said to branch from 20 to 30 feet from the ground.

In some of the *Corylaceae*, viz., *Ostrya* and *Carpinus*, the small nut is attached to a leaf-like organ by which it is drifted to some distance from the tree. This is formed from a bracteole in the female flower, which is cup-like at base, and in *Carpinus* bears, when in fruit, an elongated simple or trifid limb.

In *Ostrya carpinifolia* (the Hop Hornbeam), a native of Southern Europe, China and Japan, North America to Guatemala, the bracteole develops in fruit into a thin ovate acute papery utricle ¾ inch long and ¼ inch wide, entirely closed, inside which is the small nut at the base. These are borne in a cone about 1 inch long on the top of a twig. They are extremely light and readily blown away.

I find in Kew Gardens those from a tree about 15 feet tall are blown to a distance of 25 feet. They do not rotate as they fly, but flutter along like falling leaves. Sometimes a part or the whole of the short cone-like racemes is blown off. This may rotate a little, and is liable, from the larger surface exposed to the wind, to be blown a little further along the ground. The individual utricles when fallen usually lie flat and are not carried further (Pl. VI, figs. 11 and 14).

Carpinus (the Hornbeam) is a genus of a number of species ranging over the north temperate region, the greatest number being natives of China and Japan, and spreading eastwards to North America, as far south as Guatemala, and westwards through North Asia and the Himalayas to Europe. The fruits

are borne on a more or less elongate pendent raceme, and consist of a small dry nut subtended by a bract, of which the form and serration bear usually some relation to the adult leaf (Pl. VI, fig. 16).

There are two types of bracts. In one section it is short ovate, often serrate, inaequilateral, with no lateral lobe or only a very small single one; in the other it is 3-lobed, the lobes being long and narrow, entire or nearly so, and long in proportion to the small nut. There are, however, various transition forms between these two types. In the first series there are a number of species, chiefly Asiatic, *C. japonica*, *C. cordata*, *C. Davidii*, of China and temperate Asia, *C. faginea*, of the Himalayas, *C. caroliniana*, of North America, and *C. orientalis*, of Southern Europe; while *C. betulus* and allies form the second section.

In *C. orientalis* the bracts form a tuft at the end of the branches, each bract bearing a fruit at its base. These bracts have the form of the leaf, which is ovate serrate, but are sessile and show a tendency to produce a lateral lobe on one side at the base. In *C. japonica* and *C. cordata* they are similar, but it is noticeable that in the latter species the leaves are larger than usual, as are the bracts. The leaves, however, vary in size, and the broader they are the broader are the bracts. *C. pubescens* has small broad and inaequilateral bracts. In *C. betulus* (the European Hornbeam) and *C. viminea* the bracts are quite unlike the leaves. They are 3-lobed, the mid-lobe being the longest, all linear, narrow and blunt.

In *C. betulus* the nut is small and very light in its 3-lobed bract, to which it is firmly attached. The tree fruits late, and the leaves have nearly all fallen by the time the fruit is ripe, so that they are fully exposed to the November blasts. When they are detached they fall a short way vertically from the pendent raceme and, rotating with great rapidity, are carried to some distance. From a tree about 45 feet high in Kew Gardens I have seen fruit in a light wind fly 36 yards before alighting. But after falling they are very apt to be blown further along the ground by continuous blasts, and I have found them, after a heavy gale, to have been carried along 76 yards in open woodland and over 100 yards on a grass plot. They possess several advantages over the other section. First, the raceme is longer and contains more fruit than the others; secondly, the longer, narrower wings offer a greater surface to the wind, and the 3 wings serve to rotate the fruit vertically, so as to keep the fruit longer in the air; and thirdly, owing to the long lobe remaining more or less erect when the fruit is fallen, it is more readily blown on along the ground. *C. betulus* is very widely spread over the whole of Europe, from south Sweden to Asia Minor and Persia.

Taking as a type of the other section *C. orientalis*, we find that the whole spike is from 1½ to 2 inches long, and is compact. The bract is broad ovate, the edges serrate, with a mere trace of a side lobe, much too small to be of any use in flight, the whole bract is ½ inch long and as wide. When detached it flies flat, rotating horizontally in the wind, and will not be blown along any further unless the circumstances are very favourable. I found they flew in a fairly strong gale about 30 yards.

The difference in the distances traversed by these 2 fruits was very well shown by 2 trees side by side, about the same height and both loaded with fruit, in Kew Gardens in November, 1926. There had been a heavy south-westerly gale in the night, and the ground was strewn with fruits of *C. betulus* for over 40 yards from the tree, which was the furthest away of the two. The fruits of *C. orientalis* had not gone half as far as those of *C. betulus*, and only a very few had got as far as that.

C. orientalis is by no means as widely distributed as is *C. betulus*, ranging only along the Mediterranean from Italy to Taurus and Asia Minor. It is

perhaps worth noting that in *C. caroliniana*, of North America, which has bracts of much the same shape as *C. orientalis*, the furthest travelled form, the variety *tropicalis*, of Mexico and Guatemala, has a distinctly narrowed linear lobe to the bract and a more strongly developed side-lobe.

Ephedra (*Gnetaceae*).—These are erect, leafless broom-like shrubs, dispersed over the north temperate zone and in America, going as far south as Chili. They inhabit mountain districts and open sandy deserts or steppes. In many cases the fruits are drupaceous and often red, and dispersed by birds, but in desert species, where birds are scarce, the bracts surrounding the head of flowers become strikingly developed into wings, round, with papery edges, in *E. alata* 7 mm. wide and 6 mm. long. The fruits are correspondingly small, and the whole head is detached when ripe and blown over the desert.

E. alata grows on the sand dunes and sandy river banks of North Africa, from Egypt to Morocco and Algiers. *E. strobilacea* inhabits the deserts of Persia, and *E. Przewalskii* sandy and stony places in the steppes of Central Asia. The same form of evolution for dispersal in America is represented by *E. trifurca*, the bracts of which are smaller, 5 mm. wide and 4 mm. long, and *E. Torreyana*, both of which inhabit sandy deserts in America.

It is interesting to note that the only species in the Canaries are not winged-bract forms, but *E. nebrodensis*, *E. fragilis* and *E. altissima*, all bird-dispersed.

Scabiosa (*Dipsaceae*).—A genus of herbs growing in lowland open country, of about 70 species, chiefly European, and temperate Asiatic to India (Punjab), and Africa from Abyssinia to the Cape. The flowers are in compact terminal heads on a longer or shorter peduncle. Each flower is enclosed, up to the top of the tubular portion of the calyx, in a bract-involucel, ribbed and hairy, the free apex of which forms a cup frequently scarious with a number of awns, and resembling the sepaline cup of the Thrift (*Armeria*). In fruit this cup is often very large in proportion to the fruit, as in *S. stellata*, a native of dry spots in Morocco, where it is ¾ inch across, and acts as a flying organ (Pl. VI, fig. 5). In *S. palaestina* the involucellar cup is nearly as large, and while in *stellata* the slender calyx-lobes are long projecting and scabrid, in *palaestina* they are not as long as the cup. In *S. stellata*, as in *S. graminifolia* (*see* Kerner and Oliver, Nat. Hist. of Plants, ii, fig. 468, 8) and other species, the long scabrid sepals, much enlarged in the fruit, aid also in dispersal by being easily attached to the fur of animals. In *S. succisa* and *S. arvensis* the involucellar cup is small and takes no part in the flight of the fruit, and this is still more evident in *S. pterocephalus*, where the calyx-lobes are beautifully plumose (*see* under Plumose Sepals, p. 115). *S. atropurpurea* has a large involucellar cup, larger, indeed, than the rest of the body of the involucel, but the edges at the top are incurved and appear to play no part (unless it be in lightening the weight of the fruit) in dispersal; but its calyx-lobes, prolonged and setiform, are rigid and armed with short stiff processes, while the base of the involucel is strongly armed with forward pointing bristles on the ribs. By these means it is adhesive to cloth, hair, etc.

The most widely dispersed species is *S. columbaria*, which occurs all over Europe, with an allied species, through Abyssinia to the Cape. It has a well-developed cup, but the sepals are also long and scabrid, and it probably owes its extensive dispersal to adhesion to the hair of animals and to the clothing of human beings.

As is not rarely the case in a single genus, we have here three methods of dispersal illustrated: (1) dispersal by wind by an accrescent involucel composed of bracts connate in a tube; (2) by the development of the free parts of the calyx into a plumed flying organ; and (3) by the adhesion to fur of animals and clothing of human beings of the sepaline lobes, or the base of the involucel being armed with stiff processes; and though in many cases the fruits depend

for their dispersal on one only of these three methods, we also meet with cases in which two methods of dispersal are used, according to circumstances.

I will here point out that these three modifications are all caused by mere accrescence, or continuation of growth (after the flower has ceased to perform its function) of either the apex of the involucel, of the calyx-lobes, or of the bristles or scabridity of the involucel, or of the sepaline lobes. And this accrescence, whichever it be, makes it possible for the plant to be distributed and to find a suitable spot for growth, whether it be in a desert, to where its seeds can be drifted only along the ground, as in *S. stellata*, or in mountain ranges, where the wind can carry it through the air, as in *S. pterocephalus*, or in localities which, unlike these, are well provided with wandering animals by adhesion of the stiff scabrid sepaline lobes or the forward pointing bristles of the base of the involucel, as in *S. atrosanguinea.*

Another herbaceous genus, the fruit of which is provided with a bract wing, is *Patrinia* (*Valerianaceae*). These are erect herbs much of the habit of Valerians, with a terminal panicle of pink or yellow flowers, natives of the steppes and mountain slopes of Siberia, China and Japan. There are about 8 or 9 species recorded. The bract of the flower is very small during the flowering period and quite inconspicuous. In fruit it develops into a thin papery organ, adnate to the base only to the small 1-seeded fruit. The fruit has 3 cells, but 2 contain no seed; in fact, as so often happens in these winged fruits, the original extra ovules are suppressed. The floral bract (or bracteole) is absent in the other species of the order. In *Patrinia gibbosa*, of Japan, the bracteole is spathulate and blunt, about twice as long as the fruit; in *P. palmata*, also of Japan, it is much broader and longer; *P. siberica* has an oblong bracteole. In *P. villosa*, *P. scabra*, *P. heterophylla*, of China, and *P. monandra*, of India, the bract is circular, and the fruit, much smaller than in the preceding species, lies in the centre of it. This forms a much better flight organ than that of *P. gibbosa* and that set, and it is not surprising to find that these species appear to be much more common than the others and extend over a wider area. *P. scabiosaefolia* is not provided with this bracteole-wing at all. The fruit is larger than in any of the others, and has 3 low but fairly prominent wings on the sides.

Another herbaceous plant in which the bracts play a part in dispersal is *Blepharis glumacea* (*Acanthaceae*), a native of Rhodesia. It is a procumbent herb, found growing on the dried-up floor of a shallow pool on the veldt by Dr. R. F. Rand, who describes the fruiting of the plant (in *Journ. Bot.*, lxiv, p. 232) as follows:—" The ripe fruit is shed alongside of the plant. It is light in " weight, many chaffy bracts forming an envelope. It is easily blown about " by the wind. Within the bracts a tough rind encloses 2 seeds divided by a " septum. The seeds are plano-convex, the plane faces being opposed. The " whole surface of the seed is covered with a veining or flat white arborescent " lacing. When the seed is placed in water it sinks, and immediately these " lines spring into activity and appear as a complete environment of beautiful " pointed tentacles."

The order *Amarantaceae* contains a number of open-country plants in which the scarious bracts, sometimes also provided with long hairs, remain attached to the 1-seeded utricle and serve as wings to aid in the flight of the fruit. R. Chodat and L. Rehfous (in " La végétation de Paraguay," *Bull. Soc. Bot. Genève*, xviii, p. 252) describe a number of fruits so disseminated:—

" As to the dispersal of fruits, it is facilitated by the fact that the 1-seeded " fruits, often still enclosed in the staminal tube and accompanied by the " glumaceous flower or even 1 or 2 bracts, is made more transportable by an

"indumentum of very long hairs functioning like a plume (*Gomphrena pul-*
"*cherrima*), or the flowers are detached with short broad bracts (*G. Hassleriana*)."

Froehlichia paraguayensis has similar bracts, but no hairs. In *G. silenoides* the hair is shorter, but the perianth is well developed and spread for flight.

Glume Wings.

The grasses and sedges of *Gramineae* and *Cyperaceae* have their flowers, which consist merely of reproductive organs, with occasionally a number of setae or hairs surrounding them, subtended or more or less enclosed in small stiff bracts commonly known as glumes.

The nut or grain is seldom actually adherent to the bract, but it is often enclosed in one or more of these glumes, which sufficiently lightens the small grain or even exposes a sufficiently large area to the wind to enable it to be borne to some distance, and in certain grasses plays a very important part in its dispersal. Frequently, too, the glumes in grasses are provided with long awns, which certainly add to their flying facilities, especially in some species of *Stipa*, where they are plumed with fine hairs. The awns are also of use in attaching the glumes containing the grain to the coats of animals. But these uses I leave for the chapters dealing with these subjects. Here I merely treat of these glumes acting as wings to disperse the grain by wind.

In the *Cyperaceae*, so far as I have seen, the glumes do not act as wings. In *Cyperus*, *Fimbristylis*, etc., the grains and glumes fall at the same time separately, as the glume is not attached to or wrapped round the grain as it so often is in grasses.

In *Carex* and *Uncinia* the grain is included in a utricle, a loose convolute bract forming a kind of bag. It is quite possible that (especially in the species with large loose utricles, such as *Carex vesicularis*) these may be blown to some distance on the moorlands and open country where these plants grow, but I have very little evidence of this.

Grasses are met with over the whole world, both in the arctic regions and the tropics, and frequently, for a very large part of the flora, in open plains, steppes or mountain districts. The only places in which they are scarce or absent from are the wet dense forests of the tropical rain area and the actual sand deserts of North Africa, and some of the oceanic islands. A very large number owe their wide dispersal undoubtedly to human intervention, some to dispersal by adhesiveness to the fur of animals and down of birds, and a large number to the foliage being devoured by herbivorous mammals and the seeds being passed in the excreta, and we have evidence that granivorous birds, to a certain extent, also pass the grains of grasses unharmed.

I treat all these methods of dispersal of grasses under their special sections. Of wind-dispersed grasses we have a number which possess plumose hairs, and which I treat of under Plumed Grasses (*see* p. 137). There remains, however, a large series which have no further wind-dispersal apparatus than merely the attached glumes, but which are widely spread species.

Of the Grasses (*Gramineae*) E. Hackel (in "The True Grasses," p. 28) says :—

"In wild grasses certain parts of the spikelets or of the entire inflorescence
"fall off with the fruit. If the spikelet is many-flowered and every flower
"ripens its fruit, then its axis breaks into as many pieces as there are fruits,
"and every piece bears a floral glume and a palea. If the spike is one-flowered,
"the axis of the spikelet may separate above the empty glume, so that the
"floral glume and the palea fall off with the fruit (*Agrosteae*), or it may divide

" below the empty glume and the spikelet fall off as a whole (*Panicum*). If " the spikelets form a spike or a raceme, it frequently happens that the axis " of the latter divides, so that one spikelet falls off with each joint (many " *Andropogoneae* and *Hordeae*). Short spikes (*Triticum ovatum*, etc.) fall off as " a whole."

In many of the smaller grasses the grains become at once detached from the glumes in falling, as in *Eragrostis*, and in these they may also be dispersed by birds and human agency. But in many cases wind does play a part in dispersing these plants. I have mentioned some, under Tumble-Weeds (p. 33), in which the whole inflorescence is driven along by the wind, and the cases in which, by silky hairs or glumes or pedicels, they are drifted away is treated under Plumed Grasses (p. 137).

In many grasses, when the grain is ripe, it remains enclosed in the glume surrounding it, and shut in by the palea, as in *Poa annua*. This glume, being boat-like in shape and light, projecting beyond the sides of the grain, acts as a wing, so that the grain in it is readily blown away to a considerable distance. The grain, wrapped in glume and palea, is also light enough to be washed along by rain, and in many of the river-side grasses, *Digraphis arundinacea*, etc., the light chaffy glumes serve to carry the grain from the tall panicle into the river, where it is further dispersed.

Frequently in other grasses several empty glumes remain attached to the one containing the grain, and serve also as wings to aid in the wind-dispersal. The glumes, however, do not increase in size nor alter in shape during the fruiting stage, but remain the same as during the flowering stage.

The evolution of awns on the glumes, thin as they are, undoubtedly act to some extent as wings, offering more resistance to the wind than would be expected. They certainly add to the power of flight in *Hordeum murinum*, etc., and Hitchcock says of *Aristida fasciculata* in Kansas: " The fruit separates " from the mother-plant, the 3 awns reflex horizontally, and the wind carries " them with the barbed callus forward to catch the hair of animals and " clothing."

Hordeum murinum is mainly blown along the ground, the base of the spikelet in front, but below will be seen a record of this grass growing at a great height above the ground, where it is difficult to account for its presence in any other way than by wind.

I have mentioned under Wall Plants (p. 26) a number of grasses growing on walls and roofs where the grains in the seeds must have been blown by wind. Although these altitudes are not very great, their presence, raised well off the ground, shows how the wind can transport them. It is not probable that they ever go very high, but over plains, pastures, mountains and heaths, where they are most abundant and conspicuous, they may be blown for great distances. It is pointed out that in most grasses the panicle is tall and raised well above the ground, especially in those which can be dispersed by wind. I will recapitulate, with additions and remarks, the species I have recorded as Wall plants.

Aira caryophyllea.—On Agglestone Rock, Studland, 6 or 7 feet from the ground. A tall slender grass with a very lax panicle. Common all over heaths and mountain-sides. *Poa annua*.—I have seen this in gutters of the house 10 feet or more from the ground. A very readily dispersed plant, and one of the most common on walls. *Dactylis glomerata* and *Lolium perenne*.—These have several glumes attached to the flying grain. They occur on walls 6 or 7 feet high, and are very commonly blown along roadsides and open ground. *Holcus lanatus*.—Grain-dispersed in a pair of glumes, hairy and adhesive to clothes and animals' coats, but mainly dispersed by the wind. I have seen

paths in Guernsey covered all over for a considerable distance with the seed-bearing glumes. *Festuca myurus* and *sciuroides*.—On high walls and sandy dunes. *Bromus sterilis*.—On high walls and roofs.

Arrhenatherum avenaceum.—Is constantly wind-dispersed. It is common on the District Railway line, near Turnham Green, with other wind-dispersed plants. *Hordeum murinum*.—On towers 60 feet high (Wall Plants). It may often be seen blown along on the sides of walls in the autumn. Here the long awns assist by maintaining the fruiting glumes above the surface of the soil and offering a resistance to the wind.

Briza maxima and *Melica altissima* are mentioned by Kerner as wind-dispersed by the aid of their boat-like glumes.

Ischoemum nativitatis, of Christmas Island.—The spikelets of this grass were undoubtedly dispersed by the wind on the coral rocks by the sea. They are more or less hairy, which might be an aid. They were drifted into holes in the rocks, where they accumulated. I do not think it possible for the plant (which is peculiar to the island) to have been brought there by wind. In the antarctic islands there are many grasses of such genera as *Aira*, *Deyeuxia*, etc., which we know are wind-dispersed on continents. I think it hardly probable that these were actually brought to the islands by wind, but perhaps attached to birds' feathers. Once, however, the plants were established on the islands, they might readily be wind-dispersed all over them.

Pedicel Wings.

Flight by the aid of an enlarged flattened pedicel forming a wing rarely occurs, but it is found in the genus *Brunnichia* (*Polygonaceae*), climbing plants of North America and Africa. The flowers are borne in dense panicled racemes, the pedicels then being short and slender. In fruit they develop into a long, flat, coriaceous, linear wing-shaped organ. In *B. africana*, of Africa, the pedicel is winged on both sides and flat, 2½ inches long and ¼ inch wide, and is terminated by the enlarged sepals, which are connivent over the fruit, a 1-seeded nut. The whole resembles the fruit of *Ventilago* reversed, but is scarlet. The American species, *B. cirrhosa*, has a much smaller green fruit with a curved pedicel winged on one side only. Both plants are climbers on the edges of woods (Pl. VI, fig. 1).

Juliana and *Orthopterygium* (*Julianaceae*) are Mexican and Peruvian trees respectively, of no great height, about 20 to 30 feet, in which the female flowers are very small, 1-seeded, 4 in a small involucre, pedicelled. In fruit the pedicel develops into a broad, flat wing-like organ 2 inches long and ½ inch wide, terminated by the globose involucre containing the nuts, which are from 1 to 4 in number. When fallen the involucre dehisces, thereby releasing the nuts. There are 3 species of *Juliana* and 1 of *Orthopterygium* known. The latter has a narrower peduncle and only 3 flowers in the involucre. The fruit resembles a samara of one of the *Leguminosae* (Pl. VI, fig. 7).

Disc Wings.

The disc in such flowers as possess it, e.g., the *Disciflorae* of the *Polypetalae*, *Euphorbiaceae*, etc., consists of a circle of lobes or a fleshy ring usually surrounding the ovary. It may be between the stamens and the corolla, or between the stamens and the ovary, and in the latter case the ovary is often deeply embedded in it.

It is very rare to find it playing any part in the wind-dissemination of the fruit, but there is one case in which it does, that of *Paliurus*, a genus of shrubs of

Europe and temperate Asia to China and India. The species are usually bushes 6 to 9 feet tall, though one, *P. orientalis*, of China, attains the height of 30 feet. In the flower the ovary is embedded in a fleshy disc, but in fruit the ovary projects in a short cone, and is surrounded below by an orbicular coriaceous wing, the portion nearest the ovary rather thick, corky and, when dry, brittle, thinning outwards to a thin edge. The whole circular wing is 1½ inch or more across. The fruit, when ripe, is readily blown away from the bush or tree and along the ground (Pl. VI, fig. 9).

In *P. ramossissimus*, of China, the disc is not developed in this way, although it enlarges considerably, but the whole fruit forms a cone, the wide round end being at the top, and in some forms of the common *Paliurus aculeatus* the disc does not develop into a wing at all.

Calyx-Tube Wings.

In some plants in which the ovary is said to be inferior—that is, enclosed and adnate to the tube of the calyx—we find the tubular portion of the calyx provided with wings, so that the ripe fruit resembles those already described as winged fruit. The best examples of these are to be found in the *Combretaceae, Combretum* and *Terminalia*.

In the *Combretaceae* we get good illustrations of the evolution of wings from an apterous fruit. The genus *Combretum*, abundant in tropical Africa and Asia, contains a large number of woody climbers, of which the greater number have 2-winged fruits, the lateral wings being evolutions of the calyx-tube, which is adnate to the 1-carpelled ovary. The sepals, i.e., free parts of the calyx, are 4 or 5 in number.

Combretum trifoliatum has a 5-angled oblong fruit, not winged, about 2 inches in length. It usually frequents river banks or flooded places, and I have seen the fruit floating in the sea off Singapore. Like the fruit of *Halesia*, it may perhaps be rolled on its angles along the ground by wind where it occurs in dry places. *C. acuminatum*, a straggling bush of Ceylon, Assam and the Malay regions, has the 4 angles of the large and heavy fruit, 2 inches long, drawn further out into rather fleshy wings (Pl. VII, fig. 2). In *C. dasystachyum*, of Burma, the fruit is oblong, 1½ inch long and 1 inch wide; the seed-bearing portion is wide but thin. It is, in fact, intermediate between the heavy 4-angled forms and the light, strongly-winged forms. A Burmese variety has oval fruits shorter and broader in proportion to its length, and 1 inch long by ¾ inch wide. The remaining species, with a few exceptions, have a small seed-vessel and 4 papery wings. They inhabit edges of forest and open country, climbing over bushes and trees.

Pteleopsis is an allied genus of small African trees, the fruits of which resemble those of *Combretum*, but are usually 2-winged, and, like *Ptelea*, may have 2- and 3-winged fruit on the same spray. Indeed, in specimens of *P. myrtifolius* I find fruit with 2, 3 and 4 wings on the same branch.

Terminalia is a genus of large trees scattered all over the tropics of Asia and Africa. The fruit in some species is a large flattened drupe with rather sharp edges, as in the sea-dispersed *T. catappa*; in others it is 4- or 5-angled, the angles being, as in *Combretum*, the angles of the calyx-tube. *T. arjuna* is sharply 4-angled, with rudimentary wings on the angles (Pl. VII, figs. 1 and 5). In *T. macrocarpa* the fruit is smaller, with 5 strong wings. *T. triptera*, of the Malay Peninsula, is oblong, with 3 wings (Pl. VII, fig. 3). *T. paniculata* has a small fruit with 2 spreading butterfly wings. *T. myriocarpa* has a very small fruit with 2 small wings, and *T. subspathulata* has light fruits with 2 large papery rounded wings (Pl. VII, fig. 4). Here we have all stages from the unwinged drupaceous fruit with a large seed to the small-seeded fruit

with 2 large wings, the seed becoming smaller and lighter as the wings become larger. All the above-mentioned plants are to be found only in the Indo-Malayan region.

Terminalia subspathulata is a gigantic tree about 150 feet tall, a native of the Malay Peninsula. The stem is bare of branches for about 80 feet. A big tree in the Botanic Gardens, Singapore, about 125 feet tall, bore great abundance of the flat, oblong, rounded yellow fruit, 1 inch long and 2 inches wide across the wings, which are as thin as paper, but fairly stiff. These very light fruits, falling from the upper branches, drift along with the wind, rapidly rotating on their long axis, and even rising a little in the air if struck by a violent gust of wind.

I found that along the road or open grass plot they reached a distance of from 38 to 46 yards from the tree. In these flights they doubtlessly drifted along after they had actually reached the ground, but probably in the jungle they would go as far, as these light seeds would rest on the foliage below them and be driven on by the wind till they reached an open space between the trees, where, falling to the ground, they might have a good chance of developing into big trees.

I dropped some of them from the verandah of my house in Singapore, a height of about 17 feet to the ground. At the same time I dropped some of the sepal-winged fruits of *Shorea leprosula*, of which the basal seed-bearing portion is heavier than that of the *Terminalia*, and I found that the fruits of the latter drifted further than those of the *Shorea*, and took longer to reach the ground. They flew most irregularly when there was no wind during their fall, flying sometimes in one direction, sometimes in another, much in the same way as leaves do under the same circumstances. That they fly at all in such conditions is due to faint currents of the air, which is rarely ever quite still. In most cases when the fruit is ripe it does not actually fall till a good stiff breeze shakes the branches. In the violent wind storms which from time to time strike the lofty trees towering above most of the forest, the force of the wind must carry these light butterfly fruits a very long distance.

Under fruits of herbs wind-dispersed without possessing any modifications for such dissemination other than lightness and flatness (*see* pp. 23, 24) I have mentioned some of the thin light achenes of *Compositae*. In the readily dispersed *Achillea millefolium* the achene has a thin light edge to the calyx-tube of the fruit which doubtless adds to its flight distance. This thin edge is very much accentuated in *Actinomeris squarrosa*, a tall composite of North-West America. The plant is a bushy one about 6 feet high, and when the achenes are ripe the remainder of the perianths have disappeared, and there is only a ball ½ inch through of flat achenes, broadly winged. The whole fruit is 5 mm. long, the seed itself 2 mm. wide, and the calycine wings over 2 mm. each in width, so that the fruit is 5 mm. across. One side of the achene is flat, on the other is a strong rib or keel. When the fruit falls it usually falls on the side on which the keel is, and rests on the keel and one wing, the other being raised above the soil, so that the wind, acting upon the raised wing, can readily blow it along the ground (Pl. VII, fig. 6). I find that it goes along a smooth surface, by being blown, much further when lying in this position than when it lies on the flat side, showing clearly the use of the rib on one side. It is commonly blown to about 6 feet from the head, but doubtless often goes further.

SEPALINE WINGS.—TREES.

Plants with fruits winged by the evolution and persistence of the calyx lobes or sepals are very common. The sepals are often persistent in fruits when the rest of the perianth and stamens have long disappeared. They are

even accrescent in many fruits in which they appear quite useless. Thus in the Ebony trees (*Diospyros*, *Ebenaceae*) they increase in size and thickness during the ripening of the fruit, though most of these fruits are baccate and dispersed by birds, bats or other animals, nor is the calyx attractively coloured, nor in any way useful in dispersal. It seems probable that the greater toughness of the sepals (the function of which is to protect the more delicate petals and stamens in bud from injury by rain or dryness, or perhaps insect injury) is the reason for their persistence in the fruit of such plants as *Diospyros*, *Rosa*, etc., and their accrescence seems due to their being retained after their floral function is finished, and producing with the growing ovary a mere adventitious growth. However, we constantly find that this accrescence of the sepals in fruits plays a very important part in the dispersal of the plant.

One of the most striking groups of plants with the sepals developed into wings is in the order *Dipterocarpaceae*. These are forest trees of gigantic size, often attaining a height of 180 feet, with a stem bare of branches for 80 feet or more, and a large crown of foliage at the top. These trees seldom flower till they have reached a height of 30 feet, and usually not till they are at least 80 feet tall.

It may be noted that in the few genera of this order which do not possess sepaline wings, such as *Pachynocarpus*, *Stemonoporus*, *Monoporanda*, *Balanocarpus*, *Pachychlamys* and *Isoptera*, the trees do not attain the vast height of *Dipterocarpus* and *Shorea* (though *Balanocarpus* grows to 100 feet tall), and the fruits are dispersed more by rolling after falling, or by streams (*Pachycarpus* and *Isoptera*).

The *Dipterocarpaceae* are entirely confined to the dense lofty forests of tropical Asia and Africa, very abundant and varied in the jungles of the Malay Peninsula, Sumatra, Java and Borneo, less frequent in the islands further east, but ranging to the Philippines and New Guinea, and becoming less plentiful in Indo-China, India, and Ceylon, where the forests are less dense, and where also these valuable timbers have been extensively destroyed by man. One or more species occurs in Africa.

The 1-seeded nut is globose or oblong and, in some of the *Dipterocarpi*, of considerable weight. The sepals, quite short in the flower, in the winged fruits become accrescent, and, though they are inferior to the ovary, are very often adnate to the nut in fruit, forming a cup in *Dryobalanops*, *Dipterocarpus* and *Anisoptera*, adnate to and quite enclosing the nut.

The sepals being 5 in number, in some genera (*Parashorea* and *Dryobalanops*) form 5 equal linear stiffly coriaceous wings.

In *Pentacme* and *Shorea* only 3 of the sepals form fully developed wings; the other 2 are much shorter and ineffective. In *Hopea*, *Doona*, *Cotylelobium* and *Synaptea* there are 2 long wings only and 3 short ones, while in *Dipterocarpus* and *Anisoptera* there are but 2 fully developed wings, with 3 short rudimentary processes to represent the others.

In *Vatica* and *Pachychlamys* the wings are usually shorter than the fruit. The former are small trees with rather light fruit and somewhat papery wings, the latter has heavy fruit which is borne on rather low trees, and appears to be allied to certain *Shoreas* of Borneo in which the wings, owing to the hairiness of the fruit and the short way it has to fall, have proved ineffective as flying organs and have thus become rudimentary. A similar case occurs in *Parishia* (*Anacardiaceae*).

The only known African *Dipterocarp* is *Monotes Kerstingii*, a shrub or small tree in open savanna country. The flower has a 3-celled ovary containing 2 ovules in each cell, and when ripe the fruit contains 2 or 3 seeds. It has 4 short wings free from below the fruit. The occurrence of a second seed in the ripe fruit in other *Dipterocarpaceae* is not unknown, but the reduction to a single one is the rule. The presence of two persisting is an abnormality in

Malayan species. *Monotes* seems to be a primitive *Dipterocarp* in its low habit and the number of its seeds.

When one of these fruits falls from a lofty tree, it drops vertically for a distance of from 5 or 6 feet or more, and then the tips or as much as half of the wings spread outwards, and the fruit, still falling vertically, commences to rotate rapidly. This lessens the speed of the fall, and allows the wind to act upon it and drift it to a considerable distance from the tree before it reaches the ground. The rapid spinning round of the fruit does not of itself cause it to be carried away from the tree. A shuttlecock struck vertically into the air falls, rotating as it does so, on the spot from which it was struck.

I dropped fruits of *Shorea leprosula* from my verandah, 17 feet above the ground, when there was no perceptible wind, and they fell within 6 feet of the spot where they would have fallen if the wings had been removed. This applies to all winged fruits. I find if I drop a match and a samara of an Ash (*Fraxinus*) or an *Acer* together in a room, both the match and fruit fall in the same spot. The fruit takes longer to reach the ground, but does not go further without the aid of a light current of air.

The size and weight of the winged fruits of the *Dipterocarpeae* vary considerably. Those of *Hopea Lowii* have wings only 2 inches long and ½ inch wide, with small pea-sized fruits. The *Shoreas* have usually larger wings in proportion to the fruits. *S. macroptera*, one of the most common species, has wings 4 inches long and 1½ inch wide, the nut being ¾ inch long. *Dipterocarpus grandiflorus* has the biggest fruit of any in the order, the wings being from 7 to 9 inches long and 2 inches wide, the basal part containing the nut being 2½ inches long, and quite heavy. It possesses 5 long wing-like ridges running for the whole length of the fruit, which perhaps retard the fall of the fruit and cause it to be blown further (Pl. VII, fig. 10), and some other species (*D. Lowii*) have transverse ridges surrounding the fruit, probably having a similar effect.

There is no doubt that the lighter fruits of the *Shoreas* and *Hopeas* fly much further than the heavy fruits of the *Dipterocarpi*, and these trees are much more abundant than the latter in the Malay forests, though *Dipterocarpus grandiflorus* has a much wider distribution (from the north of the Malay Peninsula to the Philippines) than any species of *Shorea* or *Hopea*.

It does not appear that in these plants the number of wings fully developed, so as to take part in the flight of the seeds, whether 2, 4 or 5, has much influence on the distance to which they travel, at least so far as I have been able to discover by experiment. The 2-winged fruited *Dipterocarpus* and *Anisoptera* trees are not as abundant as the 3-winged *Shorea*, though the *Dryobalanops*, with 5 fully developed sepal wings, is distinctly more limited in its distribution. However, if there is any difference in the result from the number of wings, it is slightly in favour of the lesser number. It has been shown that in many cases of winged fruits the 2-winged ones have an advantage over the 3-winged.

In the thick forests the heavy winged fruits of the *Dipterocarps* and such trees, though borne by their wings some 40 to 50 yards from the tree, cannot usually progress farther over the ground, as there is rarely any wind along the ground level in the dense jungle, and if there were any, the flight of the fruits would quickly be arrested by the thick undergrowth; but in open country the lighter of these winged fruits might drift along for some distance (as the thin samaras or other light winged fruits do) by successive blasts of wind acting on them after they have fallen to the ground. As most of these light winged fruits will float in water, should they happen to fall into a river, they may be drifted for some distance, not only down stream, but if the wind is blowing up stream, actually against the current, the wings, projecting from the surface of the water, acting as sails. I have seen the fruits of *Dipterocarpus*

oblongifolius travelling up stream against the rapid current of the Tahan River in Pahang. I have also found them floating in the sea off the Tringganu coast, but all I saw there were dead. As these fruits fly so short a distance, they naturally never reach islands, being quite destroyed by sea-immersion. The very similar-looking fruits of *Gyrocarpus*, however, do resist the action of sea-water, and are consequently very widely dispersed. The number of fruits produced by one of these gigantic trees is very large, but many thousands of them are unfertilised. These barren fruits are often empty, but sometimes the seed-cavity is filled with resin. These fall first, often in great abundance for some days, after which, a week or so later, the ripe fruits begin to fall. They are generally fewer than the barren ones, but still are abundant. In all calculations I have made as to the distance of flight of winged seeds, I have taken only fully developed seed, and those at the furthest point from the tree, for barren seed will fly further than the heavier fertile ones, and though seeds fallen comparatively near the tree will germinate, it is on the ones that go furthest that the dispersal of the tree really depends. The ripe seeds when fallen are very frequently largely destroyed by rats or mice, and where, as often happens, a great part of the fruit crop falls all together near the tree, most of them are eaten by these animals. I observed this especially in the case of a *Shorea* about 30 feet tall, which, being much lower than the rest of the forest, which rose around it to a height of 100 feet, had not the advantage of the winds above, from which it was quite cut off. In loftier trees, 100 to 180 feet tall, the fruits not only fly farther but are more widely distant from each other, and these scattered seeds are less easily to be found by the rodents, besides having the advantage of germinating and developing at a considerable distance apart.

In the dense forests of the Malay Peninsula the big trees are to be found at a distance of not less than 30 yards apart. In occasional instances where I have found two such trees closer together than this, there is a correspondingly increased distance between them and the next high tree. It will be noticed that the furthest flight of these fruits is from 40 to 90 yards, and this allows them to drop well out of the area round the parent tree, which would be too near for them to develop into full-sized trees. Ripe fruits which fall and escape the attacks of animals almost invariably germinate and grow with a rapidity varying according to the density of the surrounding forest.

If the competition for light and space is too severe for the seedlings, the young trees may remain no more than 6 or 7 feet tall for many years, and most of them would never attain a sufficient height for flowering. Should, however, a big tree fall and clear a space near them by crushing most of the surrounding vegetation, the young trees take on a more rapid growth and may attain their full size.

Shorea rigida, of which there were several large trees about 100 feet tall in the Singapore Garden jungle, where the surrounding trees were about as tall, had a number of seedlings within 20 yards of its base. These were 5 or 6 feet tall when I first saw them about 1888, and were hardly 12 feet tall when I last saw them in 1915. They were always surrounded by a dense thicket of other small trees and bushes. These *Shoreas* do not flower till they are 30 feet tall, and in good circumstances only attain this height in 30 years. At this height in a dense forest, where the top level of the trees is 180 feet, and the ground covered with a dense thicket of young trees and shrubs of all kinds (where the heavier gales of wind do not penetrate), the fruits are less widely distributed than those from the full-grown trees of 180 feet tall, so that, unless there happen to be any bare spaces near, the progress of the progeny of a 30-year-old tree must be very slow.

Dryobalanops aromatica (the Camphor tree) in the Malay Peninsula, usually

at least, occurs not scattered over the forest as isolated trees, as do the other *Dipterocarpaceae*, but forms forests on certain hills exclusively, or almost exclusively, composed of adult trees and seedlings. In one forest at Kanching, Selangor, very many years ago, I could not find any trees but Camphor, nor any undergrowth but a dense thicket of seedlings. Visiting the place about 20 years later, I was surprised to see not only few or no seedlings of the Camphor, but no trees of the size which the seedlings I had previously seen should have attained to were to be seen at all, but a mixed vegetation of undergrowth, as in ordinary forests, had covered the ground. I presume that there must have been some outbreak of one of the fungus pests. Perhaps *Rosellinia radiciperda* Massee, of which I saw traces on Camphor tree seedlings in the neighbourhood, had destroyed them. This fungus spreads like fire underground in the roots of all manner of woody plants, destroying them completely and only leaving the biggest trees, Monocotyledons and Ferns.

It is rare to find forests of a single species of tree in the tropics, and *Dryobalanops* is the only gregarious tree I know of in the Malay Peninsula (exclusive of the mangrove swamps, which sometimes consist of 1 or 2 species only). One-tree associations are very liable to epidemics of insect or fungus pests. The dispersal of seeds away from each other is therefore of considerable value, and is, indeed, one of the reasons for its value. The ideal for trees in forest is that the seeds should be so widely scattered that a pest cannot spread from one tree to another, yet not so distantly that the insect-pollinators can fly from tree to tree.

In the "Annals of Botany," xix, p. 353, I estimated the rate of progress of the *Dipterocarpaceae* over the area which they now inhabit thus:—If we assume that a tree flowers and fruits successfully at 30 years of age, and that some fruits are scattered to a distance of 100 yards, that the furthest fruits always germinate and so continue in one direction, it will be seen that under such favourable circumstances the species can only spread 300 yards in 100 years, and would take 58,666 years to cover 100 miles. This seems an extraordinary slow rate of migration, yet I believe that I have overrated the rapidity. Occasional increases might occur, such as the falling of a seed on a drifting log or into the river itself, but there are few or no streams in the hilly slopes of the Peninsula which are strong enough to carry the fruits. Again, excessively violent storms of wind might carry them further than usual, but such storms are very rare. I have seen these *Dipterocarps* in fruit during as violent a windstorm as we have ever known, and even then the fruit did not fly 100 yards. Allowing for all these possibilities, it will be seen that in these calculations I have estimated the flight at 100 yards, whereas few fruit have been found more than 40 yards from the tree, nor have young trees of any age been found at a much greater distance.

I also assume that the very furthest fruit in one direction have developed into trees (whereas it usually happens that lighter and inferior seed drifts further than the heavier fertile one), and also that the violent winds always blow in the same direction when the tree is in fruit. Again, in the exceptional cases in which fruits were found at a distance of 100 yards from the parent, the tree was very much taller than the surrounding vegetation, and had a clearer line of flight than it would have had in the primeval forest, where many trees would be on the same level, and their foliage would check the flight from the fruiting trees, and, besides, trees of 30 years of age and for long after would, being comparatively low, get less of the wind than the taller century-old trees, and their fruit would certainly take a much shorter flight. In the case of a young *Shorea leprosula*, 30 feet tall, a few seeds were found to have gone 30 feet away from the tree, but no farther.

The Malay Peninsula consists to a large extent of hilly country, the mountains

rising to a height of 7,000 feet, but *Dipterocarpaceae* are not met with at much above the 2,500 feet altitude. These hills are densely forested, and it might be suggested that the fruits would fly to greater distances down hill in heavy gales. This might be so, but it must be remembered that in its migrations a species would have to fly up hill quite as often as it flies down hill, and its progress up hill would be slower. Taking all these facts into consideration, it would seem that I have not under-estimated the time taken by a *Dipterocarpus* tree to migrate 100 miles, but on the average it is probably nearly twice as long. I have assumed that the hill forests where these trees mostly grow have always been in a similar condition as to density of growth. It is quite possible, however, that at a very much earlier period the forests were more open, and the fruits could move along the ground faster than they do in the dense jungle. Still, this would not help much, seeing that in the case of a *Shorea leprosula* over 100 feet tall, in the Gardens of Singapore, on one side of which was an open grass plot, after violent winds blowing towards the plot, the furthest fruit I could find was 98 feet from the tree.

Many of the species of *Dipterocarpaceae* extend from the Malay Peninsula to Borneo and Sumatra, and some have a still further range. *Dryobalanops aromatica* occurs in several parts of the Malay Peninsula, in Borneo and the Philippine Islands. It occurs at Kanching in Selangor, on the west coast of the Malay Peninsula, and the Endau River in Johor, and Kwantan in Pahang on the east side. From Rawang to Kwantan, about 110 miles in a straight line, it would require, in the most favourable circumstances, 58,300 years, and to reach Borneo, 300 miles still further, would require 266,710 years. This seems almost incredible, but it is open to doubt if the plant migrated even at this rate.

Dipterocarpus grandiflorus ranges from the Malay Peninsula to the Philippines, and if we assume that during the period of its migration the Philippines were connected by land with the Malay Peninsula, the shortest way the tree could travel would occupy 1,500,000 years. The fruit, however, is so heavy that it could not possibly drift as far as 100 yards, nor, even in open country, could it be blown along the ground.

It is probable that these plants started from some point between these extreme distances and radiated in all directions, so that perhaps the time taken in reaching these various points might easily be halved. But these calculations are only given to illustrate how slow these winged fruits move under normal circumstances, and to show that they must have been spreading slowly over the regions they now inhabit for at least 1,000,000 years, and goes to show that this order of plants and the forest regions which these plants inhabit must be of very great antiquity.

I have already alluded to *Pachychlamys*, a genus closely allied and formerly incorporated with *Shorea*. A certain number of *Shoreas* (in Borneo chiefly) seem to have developed very large and heavy seeds which contain a large amount of vegetable oil or butter (the " Minyak Tenkawang " of the Malays, used in cookery). I cannot give any reason for the use of this oil to the seed, but it obviously increases its weight. In *P. pinanga* and *P. ghysbertiana* 3 wings are large, 3 inches long and 1 inch wide, and the other 2 not much shorter, but in *P. stenoptera*, *P. Hemsleyana*, and *P. Thiseltoni* they are quite aborted, distinctly shorter than the large heavy nuts, and practically quite useless for flight. In very young fruits they are ovate and well developed, but as the fruit grows they do not increase in length to the great extent to which those of *Shoreas* do. The trees are usually from 40 to 60 feet tall, so far as their height is recorded, so that in the forests, where the greater number of trees overtop them, they would not derive any benefit from the wind, as do the more lofty *Dipterocarpi* with heavy fruit. (Some of the species are recorded

as "very big trees," but I have no actual recorded heights.) This appears to be a case in which, owing to the largely increased size and weight of fruit and the shortness of the trees, the wings which were formerly large have become useless and rudimentary. A somewhat similar case occurs in the genus *Parishia*. I do not think that in either case the plants with aborted wings are primitive species, though it is just possible. Many trees in forests possess heavy and large fruits which are merely dispersed by falling and rolling, and in the jungle *Heritieras* (as has been mentioned) we have the case of a fruit which was formerly winged becoming apterous.

Gyrocarpus (*Hernandiaceae*).—This includes one or more tropical trees of great size, of which the fruit in a bony nut over 1 inch in diameter, with 2 spathulate narrow wings, 3 inches long and ½ inch wide, which are the accrescent lobes of the calyx, the tube of which adheres to the nut as in *Anisoptera*. It is interesting to note that while in the male flower the calyx is from 4- to 7-lobed, in the female it has but 2 lobes developed, the other lobes being suppressed even in the flower. The trees are leafless when in fruit, so that the fruits, hanging downwards, are fully exposed to the wind. When detached from the tree they rotate briskly and fly for a considerable distance. R. Rangachari says that in India they have been found nearly a mile from the nearest tree. In Christmas Island I found quite a small forest of seedlings, evidently from seeds blown from the big trees in other parts of the island. In most places, however, they grow near the seashores, and the fruits are blown into the sea, where they drift to distant coasts and to islands. This part of their dissemination is related under Sea-Dispersal (p. 313).

The *Anacardiaceae* are mostly large trees with large or small fruits, which are dispersed in various ways, and a few species have the fruit winged by evolution of the sepals. Among them are the fine trees of the genus *Parishia*, which are found in the forests of the Andamans, Burma, Cambodia, through the Malay Peninsula and Borneo to the Philippines. These trees usually attain the height of from 100 to 150 feet or more, and are leafless when the fruit is ripe. They have the habit of the big *Dipterocarpus* trees, being branchless for 80 or more feet. With one exception, the fruits are small, about ½ inch long, and light, and the sepals (4 in number) are long, thin and narrow, sometimes as much as 7 inches in length and about ¼ inch wide. One species, *P. paucijuga* Engler, has very large and heavy fruit 1½ inches long and 1 inch through, with short, erect, narrow wings hardly longer than the fruit, and quite useless as flying organs. The tree is only from 60 to 80 feet tall. (I have already alluded to this plant in treating of the genus *Pachychlamys* of *Dipterocarpaceae*.)

There are many smaller (and some tall) trees which occur in more scattered woods or in open country, which have fruits in which the sepals are accrescent and form wings. The fruits, however, are usually much smaller with shorter wings than in the gigantic *Dipterocarps* and *Parishia*. Owing to their habitat, they can be blown along the ground after falling, as their lightness and comparatively small size make this possible.

Of *Astronium* (including *Myracodruon* (*Anacardiaceae*)) there are about 12 species of small or medium-sized trees ranging from Trinidad to Paraguay. These have small 1-seeded fruits with 5 papery sepaline wings, which ripen when the trees have shed their flowers and so are fully exposed to the breezes. The trees range from 10 to 60 feet in height. The fruits of *A. fraxinifolius* and *A. concinnum* have rather long narrow wings, those of the latter 1 inch long, and the plants appear to be rather large trees, while *A. Candollei*, only from 18 to 24 feet tall, has short rounded papery wings.

Loxostylis alata, a small tree of South Africa, 15 feet tall, has small round-winged fruits. I have no clue as to the habitat of these trees, but it

appears to me that the short trees of 20 feet or so tall have shorter and rounder winged fruits than the taller ones of 60 feet or more. It seems probable that these small flat-winged circular fruits are rather destined to be drifted along the ground in open country.

Schoutenia is a small genus of Malayan trees belonging to the order *Tiliaceae*, usually from about 50 to 60 feet tall, with very numerous fruits, small and globose, surrounded by the accrescent chartaceous calyx, which, from being quite small in the flower, becomes, when ripe, of considerable size and very conspicuous. In *S. hypoleuca*, of Cambodia, the fruit is comparatively large, and the wings ½ inch long and spreading. In *S. Kunstleri*, of the Malay Peninsula, the sepals in fruit are nearly 1 inch long and free nearly to the base, and the fruit is smaller. In *S. Mastersi*, of the Malay Peninsula and Borneo, the sepals are joined into a star-shaped saucer with 5 short points, 3 inches across (Pl. VII, fig. 7).

Homalium (*Samydaceae*) is a genus of African and Asiatic trees, usually about from 25 to 30 feet tall, with rather small flowers in panicles or racemes. The fruit, which is small and few-seeded, is inferior, half-inferior or superior, and usually winged. It is interesting to note that the wings are formed of the persistent and accrescent sepals in some species, of the petals in others, and in some of both, the sepals and petals being equally persistent and equally enlarged. Thus in *Homalium grandiflorum*, of the Malay Peninsula, and *H. Damrongianum*, of Siam, the 7 to 9 sepals develop, after flowering, into a flying mechanism. They become long, spathulate-lanceolate, blunt, and somewhat spreading wings. In these the petals, too, are persistent and somewhat enlarged, but shorter than the sepals. These trees are about 80 feet tall when fully grown, and inhabit dense forests. *H. grandiflorum* flowered and fruited only once in about 20 years, and all the trees of this species in the Singapore Garden fruited at the same time.

H. undulatum, a tree of about from 40 to 60 feet tall, has, when in fruit, 5 spathulate sepals and petals, the latter about half as long as the sepals, all spread out flat in a stellate form about ½ inch across. This species inhabits limestone rocks in the Malay Peninsula.

H. Griffithianum, of the Malay Peninsula, *H. rufescens*, of the Cape, *H. stipulaceum* and *H. africanum*, of tropical Africa, and several other species, have smaller fruits winged by both the sepals and petals, from 10 or 12 in number, nearly equal in size and fringed with hairs. In *H. myrianthum*, of Borneo, the sepals and petals are, in fruit, all equal, very narrow and linear, and only $\frac{1}{20}$ inch long. *H. macropterum*, of tropical Africa, has the petals only, enlarged, and ⅓ inch in length (Pl. VIII, fig. 1).

The genus *Alberta* (*Rubiaceae*) includes 2 species, *A. magna*, of South Africa, and *A. minor*, of Madagascar. The first is a tree about 50 feet tall, growing in woods and in deep clefts of precipitous mountains. It possesses 5 sepaline lobes on the top of the fruit, which is inferior; of these, 3 are short and tooth-like, and 2 a little longer in flower. These 2 slightly larger ones develop, in fruit, into narrow spathulate wings a little over ½ inch long and $\frac{1}{10}$ inch wide. The 1-seeded fruit is ¼ inch long. The wings spread a little at the top and cause the fruit to rotate as it falls in a breeze. *A. minor* differs in having the 4 sepaline lobes developed into wings, and they are more obovate in outline. It inhabits woods in Madagascar.

Nematostylis, an allied plant also from Madagascar (*N. loranthoides*), has only 1 sepal lobe developed into a wing, but it is nearly full-sized in flower, though rather shorter than the corolla. The flowers are clustered in a head. The enlargement of 1 sepaline lobe only has a parallel in the genus *Mussaenda* (*Rubiaceae*), in which most of the species have one sepal in the central flower of a 3-flowered cyme much enlarged and coloured white or red. These do

not, however, persist in fruit, as the fruit is a green berry, but merely serve to attract insects to the inconspicuous corollas.

Grielum, a genus of *Rosaceae* in South Africa, comprises several low herbs, some prostrate with large flowers with a calyx of 5 acute lobes. In fruiting the calyx is accrescent and the lobes spread out and become ovate, forming a 5-lobed saucer-like body resembling that of *Schoutenia*. The carpels are from 5 to 10 in number, small, dehiscing at the tip and emitting a number of small seeds. The calyx with the carpels is readily detached, and can be blown along the sandy veldt on which the plants grow, scattering the seeds as it flies along.

Jackia (*Rubiaceae*) is a very handsome treelet when in flower or fruit. It is a native of open swampy ground in the Malay Peninsula and Borneo. A small tree, about 20 feet tall, with long peduncled pendulous many-flowered cymes, 4 inches across. In flower the sepals, of which 3 are larger than the others, are quite short, 4 mm. long. In fruit they increase much in length and breadth, oblong-oblanceolate in shape and widely spreading, and red in colour. The ovary contains 2 ovules, of which, as is so common in winged fruit, one is aborted. When detached by a gust of wind, they fly spinning away to some distance across the open swamp.

Abelia (*Caprifoliaceae*).—Shrubs in which the sepals, 4 or 5, are accrescent, and which range from Afghanistan to Japan across the whole extent of temperate Asia. Two species are found in Mexico, suggesting that the genus migrated from China, its headquarters, to North America, and then died out in the northern part of the continent.

Triplaris Linn. (*Polygonaceae*) is a genus of soft-wood trees of rapid growth, met with in South America, in which the unisexual flower possesses a short tubular perianth with 6 lobes, of which the 3 outer ones, corresponding to sepals, are usually larger than the 3 inner ones. In fruiting these 3 larger lobes develop into long oblong-lanceolate wings, blunt at the tips and red or purple in colour. The 1-seeded fruit is enclosed in the perianth tube, and rounded in shape. The whole ripe fruit reminds me of one of the 3-winged Dipterocarp fruits. Spruce (in "Notes of a Naturalist," ii, 402) says that *T. surinamensis* is a tree 100 feet tall or more, and of rapid growth. It is conspicuous from its red shuttlecock fruits. *T. Schomburgkiana* is a smaller tree; the highest I have seen recorded was about 25 feet tall. The fruits in this species are described as purple.

Climbers with Sepaline-Winged Fruits.

A number of climbing shrubs have the sepals developed into shorter or longer wings which spread out widely in the fruit, so that when the fruit, which is usually small and 1-seeded, becomes detached, it floats away, rotating rapidly. Most of these plants are woody high climbers inhabiting rather open jungles in the tropics. They belong to various orders. *Calycopteris floribunaa* (*Combretaceae*) has 5 lanceolate, blunt papery sepals in fruit, from ¾ inch to 1 inch long and ⅓ inch wide. The fruit itself, which is inferior, is 5-angled, only ¼ inch long. It is a native of the Malay Peninsula and India. *Petraeovitex* (*Verbenaceae*) has fruit with 5 spreading sepaline wings. There are 4 species which grow in open woods, climbing on bamboos and small trees. *Agdestis clematidea* (*Phytolaccaceae*) is a climber festooning trees in Mexico, which has a small fruit with 4 oblong-lanceolate papery sepals.

Ancistrocladus (*Ancistrocladaceae*) is a small genus of Indian, Malayan and African scandent shrubs. Their affinities with other groups of plants is obscure, but they were formerly classed under *Dipterocarpaceae*. The fruits are rather small and the 5 sepals are more or less developed into wings, their bases being adnate to the single-seeded fruit (Pl. VIII, fig. 3).

In *A. Barteri*, of Africa, which is an under-shrub 14 feet long, the sepaline wings are very short, erect and not spreading. In *A. Wallichii*, a native of river banks of Cochin China, *A. stelligerus*, *A. Griffithii* and *A. attenuatus*, all natives of India and Cochin China, the wings are stiff, short, rounded and spreading flat, much like those of *Isoptera borneensis*. Possibly these are dispersed by being blown into rivers, but I do not find anything recorded of the natural history of these plants. In *A. pinangianus*, *A. Heyneanus* and *A. extensus*, the wings are long and narrow, like those of a *Shorea*, but spreading, very unequal and spathulate, something like the propeller of an aeroplane. These species are natives of India, Cambodia and the Malay Peninsula. All the species possess powerful woody hooks by the aid of which they can climb on trees or shrubs. *A. pinangianus*, the only species I have seen wild, forms bushes on open sandy spots, usually by the sea, where there are no trees for it to climb on, but it also occurs in woods, where it climbs on trees.

None of these species appear to climb to any great height, but the possession of these woody hooks, almost useless in the sandy open spots, and the sepaline wings, well developed in *A. pinangianus* and its allies, suggest that these plants were originally lofty climbers in forest; but though this habit has largely ceased, in *A. pinangianus* at least, the plants still retain their modifications except in the case of *A. Barteri*. The wings, however, still serve to cause the fruits to drift along the ground in the wind in the open country where it grows.

In a few species of plants the calyx of the flower is large and showy, forming an additional attraction for the pollinating insects. When the flowering is over, the colour fades away and the calyx, remaining dull in tint, serves now as a wing to carry the fruit away from the plant. The most showy of these is the ornamental shrub *Holmskioldia* (*Verbenaceae*). *H. sanguinea*, of India, is a scrambling shrub in which the scarlet flowers, small and tubular, are surrounded by a broad, flat, saucer-like calyx of a brilliant blood-red, which remains after the corolla has fallen, and serves to drift the fruit of 4 pyrenes away from the plant (Pl. VII, fig. 9).

In *Petraea*, a genus of climbing shrubs of South America belonging to the same order, the calyx is usually composed of 5 linear oblong violet lobes, somewhat stiff and spreading, which set off the dark violet blue corolla in the centre. Here the fruit is 1-celled and 1-seeded (occasionally 2-celled and 2-seeded). When ripe the calyx loses its gay colouring and becomes a dirty pale brownish colour, and is soon blown off, carrying the fruit with it and being drifted away by the wind. In these plants the calyx does not increase in size in fruiting, as it is quite large enough.

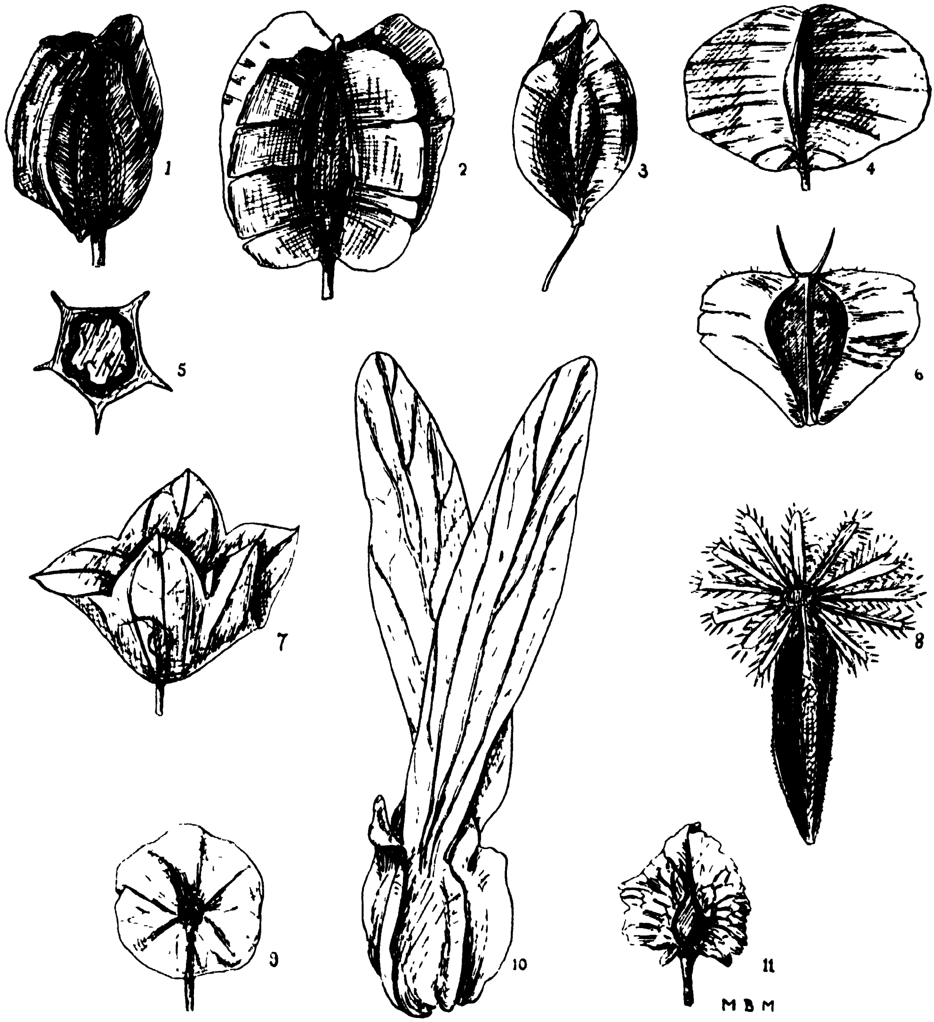
Cyanostegia (*Verbenaceae*) is a dwarf shrublet of Australia in which the calyx is saucer-shaped and slightly 5-lobed, blue and campanulate in flower, becoming flatter and larger in fruit. The fruit is unilocular and 1-seeded or bilocular and 2-seeded. It is hairy, as is the base of the calyx. This probably serves to attach it to the soil as it drifts along.

Herbaceous Plants with Sepaline-Winged Fruit.

A good many of the herbaceous plants which inhabit open country have the fruit provided with enlarged wing-like sepals which serve to aid in wind-dispersal. In these the plant is usually tall, or the panicle is raised above the basal foliage so as to readily catch the wind, and the fruit is 1-seeded. Such plants are those of the genus *Rumex*, *Oxyria*, *Rheum*, etc. (*Polygonaceae*).

The sepals in *Rumex* (except R. *acetosella*) are accrescent and enclose the small 1-seeded fruit. The Docks are usually tall plants with a leafy stem bearing a large loose panicle of numerous flowers. In the fruiting season the whole panicle dries up, the upper leaves disappearing, so that the fruit is fully

PLATE VII.



WIND-DISPERSAL. FRUIT WINGED.

FIG. 1. *Terminalia arjuna.*
,, 2. *Combretum apiculatum.*
,, 3.—*Terminalia triptera.*
,, 4.—*T. subspathulata.*
,, 5.—*T. arjuna* (in section).
,, 6.—*Actinomeris squarrosa.*
,, 7.—*Schoutenia Mastersi.*
,, 8.—*Galinsoga parviflora* (enlarged).
,, 9.—*Holmskioldia sanguinea.*
,, 10.—*Dipterocarpus grandiflorus.*
,, 11.—*Rumex crispus.*

[*To face* p. 112.

exposed to the autumn winds and is readily blown away. The genus is a very widely spread one, abundant in the north temperate regions and down to the banks of the Irrawaddy in Burma, and South America, Australia, New Zealand, Tristan d'Acunha and Hawaii. Most of the common English species arrived very early in the various colonies. R. *acetosella* was in Australia in 1802. R. *conglomeratus*, R. *crispus*, R. *pulcher* and R. *acetosella* are the most common introductions into all parts of the world.

Rumex conglomeratus is one of the most common species in Britain. Though mainly dispersed by wind, it owes some of its abundance to dispersal by river, rain-wash, and adhesion to clothes. It grows abundantly on river banks, roadsides, pastures and waste ground. The sepals are comparatively narrow, with a corky boss on each of the 3 large ones, which enables it to float when blown into the river, a means by which it is largely dispersed. On land it is blown some feet away from the panicle to the ground, and continues its migrations by being blown along the soil.

Rumex sanguineus is also a river-bank plant with a corky boss on one sepal, and the fruits are largely dispersed by being blown into the water and then drifted away. The fruit of the Water Dock (R. *hydrolapathum*) has rather broad sepals, by which it is blown into the water, and, being rather small, floats, but it is undoubtedly mainly dispersed by water.

Rumex aquaticus (R. *domesticus*), in spite of its first name, so far as I have seen, is not a river-bank plant. It has very broad rounded sepals and no elevated boss. I have generally seen it in the north of England as a roadside plant. The fruits, which are produced in great abundance, are the broadest of any British species.

In *Rumex nigricans*, of India, the boss almost completely covers the sepaline wing, though in some forms the sepal edge is developed into a spiny wing. In *Rumex halophilus*, of Australia, the sepal wings also are almost entirely covered with the boss, and this is carried to excess in R. *neglectus*, of New Zealand, where the sepals are entirely thick and corky.

The boss is formed by the thickening of the midrib of the sepal, beginning first at the base, and in evolution extending to the whole length of the sepal, and eventually entirely covering it. As there is rarely any trace of it in the sepals of the flower, its evolution must be destined for the dispersal of the fruit in some way, and as it is very light and loose in texture, it seems impossible to consider it as destined for anything else but a floating organ, and we can have no doubt that in the seashore species, R. *halophilus*, R. *maritimus*, and R. *neglectus*, where it is excessively developed, it plays a great part in the sea-dispersal of these plants. It occurs, however, in some inland species dispersed only by wind, and possibly then serves simply as an anchor to arrest the flight of the fruit in a suitable spot. It is noticeably quite absent in the Sorrels R. *acetosa* and *Oxyria*, in which the broad-winged fruit is blown over pastures and mountain-sides (Pl. VII, fig. 11).

The Mountain Sorrel (*Oxyria reniformis*) has a slender panicle of fruits like those of *Rumex acetosa*, large, round and thin. In the arctic regions the panicle is often very short, but the winds there, sweeping low on the ground, serve to disperse the seed. In the mountains of temperate Asia, Europe, and North America it is taller, and there is a form in China, *elatior*, which is over 1 foot tall. These are quite tall enough to receive the full blast of the mountain winds.

Another point to be noticed in the Docks (*Rumex*) is the laciniation of the sepals in many of the species. The edges are provided with from two to several projecting spines. These rarely appear on the sepals when in flower, and when they do they are very short and rudimentary. They are quite unrepresented in the Sorrels *Rumex acetosa*, *Oxyria*, etc., and are strongly

developed in R. *maritimus*, R. *pulcher*, R. *palustris* and R. *obtusifolius*. They are most prominent in R. *maritimus* var. *Fargesii*, of South America. The Docks which have these spiny sepals usually grow in dry open spots, waysides, or cultivated land, and although some are recorded from wet spots, they are not river-bank species. The spines may serve to arrest the fruit in its flight along the ground. R. *dumosus*, of Australia, has triangular sepals, thorned, with spines on the edges. It is reported to grow on fertile lands which are subject to inundation, and its spines may be intended to attach it to the mud as the water gets shallow, and so prevent it from being carried away into deep water.

Rumex nepalensis, of India, has hooked spines, and is doubtless dispersed by adhesion to birds and beasts—a distinctly continuous evolution towards animal-dispersal.

Many of the common English spiny-sepalled Docks adhere to clothing as one passes by them, though this may not be a common form of this class of dispersal; but I have received wool from New Zealand containing fruits of R. *conglomeratus* (*see under* Plants Dispersed in Sheep's Wool, p. 605).

To sum up, the Docks and Sorrels owe most of their wide distribution over the surface of the earth to wind either blowing the fruits, by the aid of their enlarged sepals, along the ground, or from mountain peak to mountain peak; or, in the case of riverside species, into the water to be drifted down the river till they come to rest on a suitable spot on the bank. In some cases the edges of the sepals are spiny, which serves to attach them to the mud on the going down of the water, and these spines may be so far developed as to attach the fruits to passing animals to be borne away by them, and frequently the median vein of one or all sepals becomes dilated into a float, and assists in its dispersal by water. *Rumex acetosella*, unprovided with winged sepals, depends for its dispersal on the lightness of its little nuts, which are blown away by the wind, and Guppy shows, from the fruits of species he has found in the stomachs of partridges, that some can be distributed by birds. Further, he shows that the fruits of many species float a long time in sea-water, and there is no doubt that they owe their dispersal to Hawaii and Tristan d'Acunha to sea-transport.

In the mountain Sorrels (*Oxyria*) and the lowland Sorrels (*Rumex acetosa* and its allies) the floating boss is quite absent. The plants are comparatively low herbs, and occur on mountains, hill-sides, or open pastures. They have the sepals much expanded in fruit, rounded, very thin, usually about ¼ inch across. R. *acetosa* inhabits grassy pastures to a height of 1,100 feet in India. R. *hastatus*, a much-branched half-shrubby and twiggy species, grows on dry mountain slopes at a height of from 4,000 to 6,000 feet. R. *sagittatus*, a scandent species scrambling over bushes in South Africa in open country, has similar fruits. R. *vesicaria*, of India, has larger fruits, 1 inch across, the sepals being very thin. This inhabits waste ground and cultivated fields, and as it is grown and eaten as a pot herb, it has to some extent been further dispersed by human agency. The little Sheep-Sorrel (R. *acetosella*) is a much smaller and shorter plant, and the fruits are not winged. The sepals hardly enlarge at all in fruit, and, though persistent till it is ripe, merely wither over the nut and become quite dry. They seem to play no part at all in its dispersal. The very small fruit, however, is certainly blown to a considerable distance by the wind, as I have found it on rocks at some height from the ground. It has also been widely spread by human agency. Unlike other species of the genus, it spreads extensively by underground rhizomes, hence it occurs in many places in very great abundance.

The Docks owe their wide distribution all over the world to the numerous means of dispersal which they possess. In open country the fruits are blown

along by the wind, many have adaptations for floating on rivers and even in some cases on the sea. By their spiny edges many are attached to the wool of sheep or hair of wandering animals. There is little doubt that the angled nuts sometimes adhere to the feet of wading and aquatic birds in mud, and they are often swallowed by ducks and other birds, and so are transported. A considerable number of species have been carried by man to different parts of the world in grain or cultural seed. They are plants of cold temperate or subtropical regions, but are absent from the northernmost parts of the world. They can inhabit deserts, open country, river banks, seashores, hill-sides and mountain slopes up to considerable heights. With this choice of habitats and their varied dispersal mechanisms, it is no wonder that their distribution is so extensive. Very similar to the sepaline wings of the Docks are those of several species of *Polygonum*, of *P. convolvulus* and *P. compactum*, *P. cuspidatum*, *P. sachalinense*, and others, herbaceous shrub-like plants 4 to 6 feet tall.

Atriplex hortense (*Chenopodiaceae*) is also a tall herb, from 1 to 6 feet in height, which has similar thin winged sepals. It is a native of Europe and temperate Asia, recorded as growing chiefly in cultural land. The orbicular winged fruits, resembling those of *Oxyria*, I have seen blown away from a 6-foot plant for 10 yards.

In most species of *Atriplex* the sepals are green, small and fleshy, and not accrescent, and are to some extent dispersed by small birds, which eat the fruit and pass the seeds. In the Australian salt bushes *A. paludosa* and *A. Drummondi* the more or less orbicular sepals are fleshy or corky, and probably serve as floats in the sea.

In the Scabious (*Scabiosa*), as has been mentioned under Bract Wings (p. 97) most of the species use an involucel as a flying organ, a modified bract or number of bracts connate into a cup, but in some species the sepals perform the function of the involucel, as is the case in *S. graminifolia* (as is shown in Kerner and Oliver's "Natural History of Plants," ii, fig. 468, 8).

In some of the *Compositae* also the sepals (the free portion of the calyx-tube) form a parachute-like flying organ. In *Galinsoga* the sepals form small scale-like wings, which are not connate, as in *Scabiosa* or *Armeria*, but as they touch or nearly touch each other, they form a kind of parachute organ, resembling the feathers of a shuttlecock (Pl. VII, fig. 8).

In the Thrift *Armeria* (*Plumbagineae*) the calyx-tube surrounds the utricle, which encloses 1 seed. In the Thrifts the flowers are in a dense head, quite like the Scabious, while in *Statice* the inflorescence is a loose upstanding panicle. The calyx-tube above the ovary forms a papery entire parachute, and as the head of the flowers in the Thrift breaks up, the fruits are blown away, and, in gales, may drift to a considerable distance (Pl. VIII, fig. 2). In both of these genera they are frequently blown to the tops of cliffs over the sea, where the little fruits, becoming fixed in crevices, readily grow. Many of the Sea Lavenders (*Statice*) are inhabitants of steppes and open country, where their fruits are easily blown along the plains. When fallen the little fruits lie on their sides supported by the edge of the sepaline parachute, and can be readily blown further along the ground by the wind striking the upper edge, and so continue their progress. The Thrifts, which are also mountain plants as well as maritime ones, have rough hairy calyces which are adhesive to clothes and the fur of animals, and also the down of birds (referred to again later), and may be carried about the cliffs by being attached to sea-birds, but they are mainly wind-dispersed. They are plentiful in the north temperate and the Arctic regions of both worlds, descending the western mountain ranges of America to the Falkland Islands and Hermite Island, Cape Horn. Their presence on some of the Arctic and southern islands suggests that they

are carried to some extent by sea-fowl, the fruits being embedded in the down.

Statice and the allied *Limoniastrum* and *Acantholimon* range over the north temperate zone in deserts, mountain slopes and seashores. *Statice* is well represented in the Canaries, abundant in Europe, temperate Asia to China, Japan, Formosa, North India, Australia, Isle of Pines, East Africa, Socotra, Perim Island, Comoro, South Africa, West Indies, Chile and western South America. These plants, like the Thrifts, seem to get readily to islands, though not to long distances, except in the case of *S. Lefroyi* in the Bermudas. The fruits are glabrous and are hardly likely to become attached to birds' plumage, and it is unlikely they are dispersed by wind over sea.

Corolline-Winged Fruit.

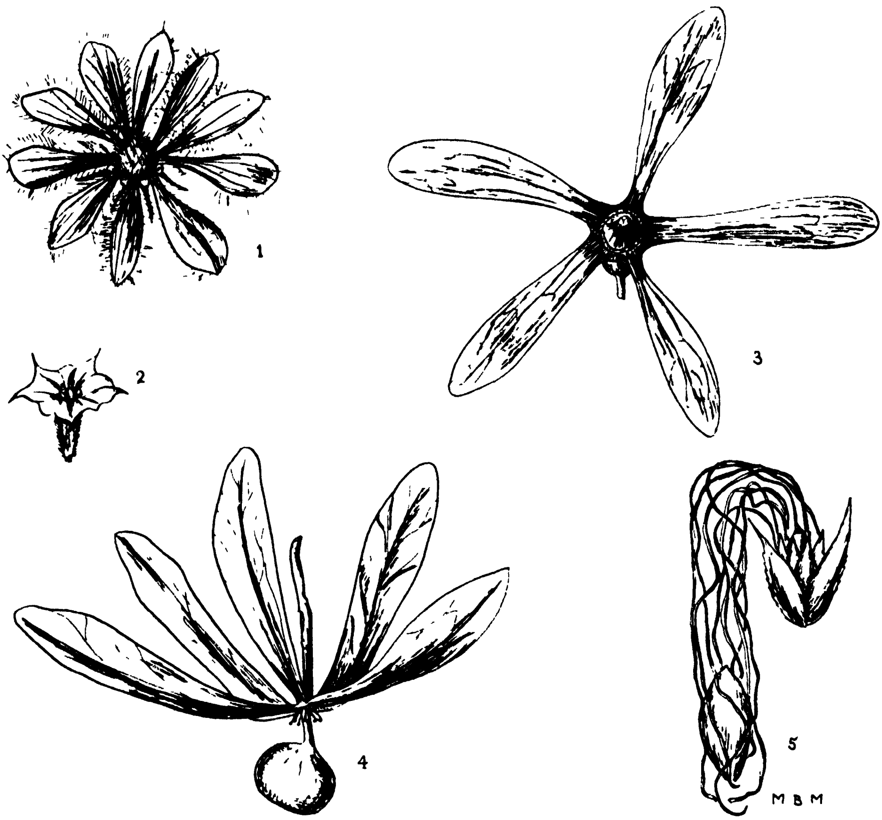
Cases in which the corolla is modified or utilised as a flight organ are more rare than those in which the calyx is adapted for flying. There are, however, a number of interesting examples. Many of them belong to the big trees of *Melanorrhea* and *Swintonia* of the order *Anacardiaceae*, and natives of the tropical forests of Indo-Malaya. In *Melanorrhea*, of which 5 out of 10 known species are provided with corolline-winged fruits, they are gigantic trees. The drupe is small, more or less globose, and black, and borne on a short pedicel above the 5 linear pink or red wings, which are the accrescent petals of the flower. In *M. Wallichii* the petals in flower are white-woolly, lanceolate, about ½ inch long. In fruit, they grow to over 2 inches long and ½ inch wide, linear-lanceolate and bright red pink. The drupe in this species is sessile, or nearly so, on the petals, but in *M. Curtisii* the gynophore is about ½ inch long, and in *M. pubescens* over ½ inch long (Pl. VIII, fig. 4). In *M. Wallichii* the fruits are produced in such abundance and are of so bright a red that it is possible to detect a tree in fruit from over a mile distant. When it falls the whole fruit turns over, so that the drupe, uppermost on the tree, becomes the lowest part, and in its descent rotates rapidly. The species with petal-winged fruits are the *M. usitata*, of India, and *M. Wallichii*, *M. Woodsiana*, *M. Curtisii* and *M. pubescens*, of the Malay Peninsula forests. In the remaining species of the genus the petals are caducous and the fruit is a simple unwinged drupe.

In *Swintonia*, a Malayan genus of big trees of which 10 species are known, the drupe is winged as in *Melanorrhea*, in all the species of which the fruit is known. It is small, round, oblong, ½ to ¾ inch long, green, with the accrescent petals from ¼ inch long in the low mountain tree *S. Robinsonii*, to 2¼ inches in the gigantic tree *S. spicifera*. The petals are not coloured in the fruits as in *Melanorrhea*, but are dull brownish-green, and are about twice as long as they are when in flower.

In *Melanorrhea* the calyx is spathaceous and caducous, so that it can play no part in dispersal, but in *Swintonia* the very small separate sepals are persistent, though they have no influence on the flight of the fruit.

Dombeya (*Sterculiaceae*), a genus of shrubs and trees of no great size, inhabiting Africa and Madagascar, has, in some cases at least, corolline-winged fruit. The corolla, usually large and showy, is persistent, and becomes dry and papery, and acts as a flight organ to the capsule. In *D. reticulata*, of Nigeria, the 5 petals are oblong, broad at the tip and narrowed to the base. The capsule is 5-celled, with 1 or 2 seeds in each cell. The plant is a shrub or small tree about 8 feet tall, and the flowers are borne in a corymb. The petals do not increase in size in fruit, but seem to become dry and papery. They are ½ inch (1 cm.) long. In *D. senegalensis* the flowers and fruit are borne while the tree is leafless, so as to be readily blown away by the wind. The capsules are small, much shorter than the corolla-wings, and dehisce, probably

PLATE VIII.



WIND-DISPERSAL. FRUITS WINGED.

FIG. 1.—*Homalium frutescens* (enlarged).
,, 2.—*Armeria maritima* (enlarged).
,, 3.—*Ancistrocladus extensus* (enlarged).
,, 4.—*Melanorrhea Curtisii.*
,, 5.—*Gahnia xanthocarpa* (with stamens).

[*To face p.* 116.

scattering the seeds in their flight. The trees are found in open savanna country or on the borders of woods. The genus is large, though local. One and probably more species than the two mentioned are dispersed by wind in this manner, but there is no information on the subject.

In *Homalium* both the sepals and petals often act as flying organs in the fruit, described under the account of sepaline wings. (*See also* p. 110.)

Another genus in which the corolla acts as a flight organ is that of the Heaths (*Erica*). These shrubs are most abundant in South Africa, and reappear in Europe, 2 species, *E. arborea* and *E. scoparia*, occurring also in Morocco, Madeira and the Canary Islands. The very small seeds are contained in a capsule, which dehisces inside the persistent tubular papery corolla. When ripe the corolla is detached, in some cases with the pedicel, and is blown away. The seeds escape either by the mouth of the corolla or by its partially decomposing. The species (very numerous in South Africa) are inhabitants of open sandy spots, rocky places, or moorland country.

The flowers of *E. scoparia* and *E. arborea* are very small, and lateral on the branches. They are certainly very readily blown away, but it is doubtful if they are light enough to reach Madeira and the Canaries by wind across the sea. However, there is no doubt of their continental dispersal by wind.

Calluna vulgaris (the Heather) is dispersed in a similar way, but the flower is not tubular, and the sepals are larger than the petals, and are the most important agents in dispersal of seeds. Both petals and sepals curl over the capsule and protect the seeds from falling out before the flower is blown away from the stem, which does not occur until the following spring.

The Heather occurs over nearly all Europe as far as Iceland, and in Morocco and the Azores and in North America (probably introduced by man), in Cape Breton, Nova Scotia, Newfoundland and Massachusetts. In these plants there is no accrescence nor any special adaptation of the petals for transport of the seeds, which remain loose in the withered but stiff petals.

Among other plants in which the corolla takes part in the dispersal of the seed are some of the clovers, e.g., *Trifolium medium* and *T. repens*. In these low herbs the corolla does not enlarge, nor is it modified in any way as a flying organ, but it persists in a withered state, dry and scarious, and encloses the pod, which contains 1 or 2, or as many as 6, small globose seeds. The withered flower becomes detached from the head of flowers, and is blown away along the ground by the wind.

A similar case is that of *Poterium obtusum* (*Rosaceae*), of Japan, a tall plant with a dense cylindrical spike of flowers on long slender peduncles. In this, too, the petals, after withering, remain attached to the 1-seeded fruit, and aid in its dispersal.

In some species of *Eriocaulon* the petals remain attached to the fruit and serve as wings in dispersal (*see* under Plant Dispersal by Water, p. 236).

Stamens as Flying Organs.

The genus *Gahnia* (*Cyperaceae*), chiefly natives of Australia and New Zealand, but of which 2 or 3 species are spread as far as the Malay Peninsula and Annam, are coarse, tall sedges, often with a dense black panicle of spikelets over a foot long. The nuts, about 4 mm. long, are usually yellow or red, and are surrounded at the base by stamens, of which the filaments are very long, increasing in growth as the fruit ripens. Wilson Saunders (in *The Gardeners' Chronicle*, December 13th, 1873) suggested that these long persistent filaments serve to disperse the fruit, acting as plumes. They are, however, readily detached from the nut, and not light enough to act in this way. It appears to

me that their use is to hold the nuts out free from the panicle so that they may be exposed to the wind. The long filaments from the base of the nut become entangled together, so that the nuts, instead of falling altogether, are suspended on the surface of the panicle. In the species with compact spike-like panicle (*G. tristis*, etc.) the filaments do not increase in length in fruiting, but in *G. psittacorum* and *G. xanthophylla*, the filaments do become accrescent, and in some cases remain attached to the nut sufficiently long to carry it to some distance. In the Malayan *G. javanica*, a high mountain plant, the stamens apparently increase in length in some plants, but not in others. It is to be noticed, however, that the nuts are, in most cases, conspicuously yellow, or, in *G. psittacorum*, red, and contrast strongly with the black panicle, so that it is possible that this arrangement of the nuts hanging free from the glumes in a tangled mass of accrescent stamens, may be intended for the attraction of birds (Pl. VIII, fig. 5).

WINGED SEED.

A very large number of plants, especially trees, shrubs and lofty woody climbers, possess seeds furnished with a wing which is an outgrowth of the testa. By the aid of this wing, when shaken out of the capsule, cone or pod, they are drifted away from the parent plant in the same way that a winged fruit is dispersed. Seeds which have a terminal or subterminal wing, as in *Pinus*, rotate as they fly; those with a thin circular or double lateral wing drift away more like a dead leaf.

The testa may be entirely very thin and reticulate, or the wing may be formed by an evolution of the raphe of the seed (the attached part of the funicle), but occasionally, as in *Uncaria*, part of the funicle itself adds to the wing.

In the *Coniferae*, *Pinus*, etc., the wing is often formed from a portion of the ovuliferous scale, an inner layer on its face. In *Glossocarya* (*Verbenaceae*) the valves of the capsule actually remain attached to the seed and form wings to it.

We have every stage of evolution of the winged seed, from the minute seed, dispersed by its lightness, to the well-developed winged seed. In the Orchids, with the lightest seeds of any flowering plant, the minute embryo is wrapped in its thin, loose coat of testa, which varies in spread in different species (*see* Pl. III, figs. 3, 4, 5, 10).

Many very small seeds of herbaceous plants, besides Orchids, can be blown by wind to a considerable distance, although they are not winged by any modification except their small size. Their dispersal by wind entails their habitat being open country. It would not be effective in forests, nor in spots where violent storms did not occur at the time of ripening. In *Lilium* and *Gladiolus* the seeds are flattened and thin, with a somewhat corky, light testa distinctly prolonged in many cases beyond the embryo. There is, however, nothing that can be called a wing, but when the wind strikes the capsule, dehisced at the top, the seeds are thrown out a few at a time, and fly horizontally for some feet. It is conceivable that they might drift far in gales on mountain tops or over the veldt, but they could not cross an arm of the sea. Indeed, wing-seeded plants are just as absent from oceanic islands as are wing-fruited plants, though with some possible exceptions (*see* p. 71).

Melochia arborea, a tree common inland in Indo-Malaya, with samaroid winged seeds, I found in Christmas Island; but while there is no doubt that inland in the Malay Peninsula it is disseminated by wind, it has reached Christmas Island by sea, as the seeds, which are $\frac{1}{8}$ inch long, readily float. Like *Casuarina*, whose little fruits resemble the seeds of the *Melochia*, it has been spread both by wind and water.

The size of the winged seed varies usually in proportion to the size of the capsule. Small rounded capsules usually have numerous small rounded seeds, and elongated capsules, in which the dehiscence is at the top only, commonly have seeds of a simple samara shape, with only an oblong terminal wing. The number of seeds in the capsule varies from one in each cell (*Syringa*) to innumerable ones in *Uncaria* and many other plants.

The earliest winged seeds I have any record of are the curious seeds known as *Samaropsis* (*Cardiocarpales*) of the Permo-Carboniferous era. These seeds have circular or rounded wings. In one species the seed quite resembles the fruit of the Birch, in another the top is entire, rounded acute, while the base has two acute divaricate lobes. The plant producing them does not appear to have been identified with the fruits or seeds, but it is interesting to find so early a tree or tall shrub (for such it must have been) in which the seeds were wind-dispersed, much as are the Birches of our open heaths at the present day.

In many cases plants possess capsules containing minute seeds, narrow, more or less drawn out into points at the tips, which are readily blown by the wind to considerable distances. They are not, strictly speaking, winged, but they distinctly lead up to the long-tailed or winged seeds as represented by those of *Uncaria* or *Buddleia*.

An example of this is *Duabanga sonneratioides*, a tall tree 100 feet high, with long pendent branches and a round capsular fruit about 2 inches through, containing innumerable linear cylindric seeds 0·05 inch long and narrowed to a point at each end. The long points are pithy and blunt. It is an inhabitant of forests in India, Burma, and the Malay Peninsula. In India, Troup states that the seeds ripen in May, and Gamble (*Indian Forester*, iv, 1878–1879, 245) describes the profusion with which seedlings come up on the sides of old charcoal kilns at Darjeeling. The seeds in some cases have come from at least ½ a mile away from the nearest adult plant. In the Malay Peninsula it is widely scattered, but not common. The trees are sporadic, at some considerable distance from each other. It appears to prefer loose open soil, which is not to be found in a large quantity in the dense tropical forests; but the very numerous, minute seeds blown across the jungle may here and there find a suitable spot for growth, and so carry on the spread of the plant, though in these forests far the greater number of the seeds must perish for want of a suitable growing spot.

Another big tree which possesses light seeds without distinct wings is *Tetrameles* (*Datiscaceae*). This is a gigantic tree, which produces long, pendent racemes of small oval capsules ¼ inch long, opening at the top and containing an abundance of very minute seeds, in which the testa is loose, oval, reticulate and toothed. When its fruits ripen, the tree is completely leafless, and thus the seeds as they fall from the capsule are exposed to the slightest breeze through the bare branches, and are consequently carried to long distances. There are 2 species, one of which, *T. nudiflora*, has a wide area of distribution, being found in India, Siam, to the north of the Malay Peninsula, Sumatra to Celebes, and in the Andaman Islands. The other species is found from Java to the Philippines.

Forms of Winged Seeds.

Winged seeds are of various forms, depending to a large extent on the shape of the capsule and its method of dehiscence. One of the common forms resembles the fruit of *Acer*, or the nut of *Casuarina*, a long, straight or oblique, or falcate terminal wing, the more or less flattened seed at the base, a samaroid form. More rarely the wing, of a similar shape, is at the base of the seed. In

these cases, occasionally it appears that the wing is an evolution of the funicle. In another form the flat seed has a wing at each end, the seed being in the centre of a linear or oblong testa. In many fruits the small seeds have the testa more or less drawn out to a point at both ends, and the seed can hardly be called winged, but we have all stages between this flattened drawn-out seed, to a distinct wing, often thin and reticulate at each end. In some cases the wing is drawn out to a long point, so slender that it almost resembles the hair-like processes at both ends of the seed of *Aeschynanthus* (Pl. III, fig. 8 ; Pl. XI, fig. 7).

Many seeds also have a flat thin wing entirely or almost entirely surrounding the seed, a kind of circular samara ; or we may have this wing fringing both sides of the seed, but not completely covering the top and bottom of it, as in the butterfly seed of the *Macrozanonia*.

There are all stages between a mere crest round the edge of a circular or reniform seed, and a thin, papery, delicate wing. The texture of the wing also varies greatly. In *Pterygota* (*Sterculiaceae*) it is almost woody ; in *Cedrela*, and many others, coriaceous ; while in the *Cucurbitaceae* and *Bignoniaceae* it is as thin and transparent as a piece of tissue-paper. Different forms of wing may be found, not only in plants of the same order, but even in those of the same genus, and there are cases in which some seeds in the same capsule are winged and others are not. Generally speaking, however, allied plants have the same form and texture of wing.

The size of the winged seed depends mainly on the size of the capsule, and varies from the minute seed of *Galeola* and *Pterospora*, about 1 mm. across, to the great terminal wing of *Pterygota*, 8 cm. (4 inches) long and 3 cm. (1½ inch) wide, or the butterfly-shaped seed of *Macrozanonia*, 10 to 12 cm. (5 or 6 inches) across. These two latter seeds are the biggest winged seeds I know.

Samaroid Winged Seeds.

These are the seeds in which the wing is subterminal, rising from the side of the seed and prolonged into a linear or oblong lobe, as in the fruit of the Maples (*Acer*). In nearly all cases they are found on tall or moderately tall trees, and are enclosed in long pendent woody capsules, opening at the top into 4 or 5 lobes, so as to let the seed fall out gradually when the wind blows the capsules and allows the seeds to fall, rotating vertically away. A similar arrangement is found in the Pines, in which the seeds are released by the separation of the scales of the cones. The wings of the samaroid seeds may be thin and papery, but are usually stiff and almost woody.

Typical seeds of this type are those of the genus *Cratoxylon* (*Hypericineae*), small tropical trees of Asia, in which the foliage is usually fallen when the fruits are ripe, and so the seeds have a clear flight from the trees. In *C. arborescens*, however, the wing completely surrounds the seed ; it is much the largest species of the genus. *Ixonanthes* (*Lineae*), *Swietenia*, *Cedrela* and a few other genera (*Meliaceae*) ; *Gordonia* (*Ternstroemiaceae*), *Xylomelum*, *Banksia*, and a number of other *Proteaceae*, of Australia, *Lophopetalum* (*Celastrineae*), *Pterospermum* (*Sterculiaceae*), have fairly large samaroid seeds in long capsules, usually opening at the top into a number of valves (Pl. IX, figs. 1 and 2).

In the *Coniferae*, *Pinus*, *Picea*, *Abies*, *Agathis*, *Larix*, *Cedrus*, etc., the seeds are usually samaroid-winged. The size of the wing in proportion to the size of the seed varies a good deal, and in some species of *Pinus* (*P. koraiensis*, *P. cembra* and *P. albicaulis*) the seeds are not winged, and the cone does not dehisce, but is carried off and broken up by nut-crackers and rodents. In the *flexiles* group of Pines the seeds are also wingless, but the scales of the cone

are deflexed or spread, so that the seeds can fall out. A. M. Prentiss (in *Bot. Gaz.*, xiii, 1888, 236) says that the cones of many species are very sensitive to rain and general wet, and when ripe, if the weather be dry, fold backwards and forwards to let the seeds escape, but they open and close in wet atmospheres many times before all the seeds are shed. In *Tsuga canadensis* he found that in rain the cones closed up in 12 minutes. The action of the scales serves to loosen the winged seed and, by shutting and opening, to ensure the transport of the seeds in different directions by the varying winds.

P. muricata requires the actual heat of a forest fire to induce it to open its scales and release the seeds.

These winged seeds rotate very briskly in the wind. I observed the flight of the seeds of *P. laricio* in Kew Gardens in March. The seeds, which are very light, flew in a moderately strong breeze from the north to a distance of 80 yards southwardly, while, as the wind fluctuated, some went in a northerly direction for 50 yards. The tree was on a grass plot and about 40 feet tall.

Pinus excelsa, of the Himalayas.—Troup states that the seeds of this Pine weigh 7,500 to the pound, and in natural reproduction they fly to a distance of 200 yards from the parent tree.

Pinus longifolia, the Chir Pine of the Himalayas.—The seeds weigh 350 to the ounce, and fly a considerable distance. The seeds germinate quickly and so escape the attacks of pheasants, which those of the blue Pine and *Cedrus Deodara* do not, as they remain on the ground through the winter.

Cedrus Deodara, the Deodar of the Himalayas.—The seeds weigh 200 to 250 to the ounce. They are winged, like those of the Pines, but much of the seed falls with the scales of the cones, close beneath and around the base of the trees, differing therefore from the seed of the Pines, in which the seed is shaken free from the scales which do not fall with it. The dispersal apparently depends mainly on the amount of slope down which it may fall. Those of *C. atlantica* fly on the level about 80 yards.

The 3 species of Cedar, *C. Deodara*, *C. libanotica*, and *C. atlantica*, are inhabitants of mountain regions, and the limited area of the genus compared with that of *Pinus*, which is distributed all over the cooler parts of the world, is probably largely due to the inferior means of dispersal of the seeds.

Pinus Taeda (Loblolly Pine).—Of this American Pine, W. D. Sterrett (U.S.A. Dept. Agric., 1914, ii, p. 7) states :—" In general, Loblolly Pine " can be relied upon for thickly stocking in one season unobstructed areas " adjacent for a distance of 100 feet to 100 yards, according to height of trees. " Trees with many cones will scatter seeds very plentifully to a distance of " twice their own height."

Pinus alba (the White Pine of America).—E. H. Fotheringham (*U.S.A. Agric. Bull.*, 13, 1914, p. 15) says of this Pine :—" Trees on high windy slopes " may shed their seeds to ½ a mile or even more over the adjoining lowland. " On level land, when unobstructed by tops of trees, they fly usually between " 100 and 200 feet."

Pinus contorta (Lodge-Pole Pine).—D. T. Neason (*U.S.A. Agric. Bull.*, 154, p. 11), writes :—" Clements states that the distance to which seed is carried " was never found to exceed 164 feet."

Hippocratea (*Celastrineae*) is a group of woody climbers of East Asia which have flat capsules with only 1 or 2 seeds in the cells, which seeds are samaroid. Some of the species grow close to streams, and I suspect that the seeds are blown into the water and so dispersed. Others inhabit open slopes of hills, and the seeds can be distributed by wind over the open country

Samaroid seeds are not, however, very common in climbers. In most species of *Dioscorea* the seed, always winged, is winged on both sides, so having a rounded outline, the wings being very thin and papery. In one

section of the genus, *D. elephantopus*, *D. nipponica*, etc., the wing is subterminal, i.e., samaroid with the seed at the base, and in *D. triphylla* it is reversed, the wing being at the base. The oblong, not rounded, form of the capsule is responsible for the shape of the wing in these cases.

Terminthodia (*Rutaceae*) is a genus of low shrubs with small coriaceous winged seeds in little oval pods opening by a single slit. The plants are found on mountains in the Malay Peninsula and New Guinea. Allied to the tree *Evodias*, with round polished seed in the rounded capsule, these low mountain shrubs seem to have evolved a wing to allow the seeds to be blown along over the low dense vegetation of the mountain tops.

Pterygota (*Sterculiaceae*) is a big tree in which the follicle, opening by one slit along the upper edge, releases a number of large, rather heavy, almost wooden-winged seed. This seems to be an evolution from the large genus *Sterculia*, in which the seeds are usually bird-dispersed (*see under Sterculia*, p. 83), which has arisen from the scarcity of frugivorous birds in the Indian districts in which it grows, or, from the height of the tree, its not being visited by birds.

Lagerstroemia (*Lythraceae*).—These big and showy trees, with more or less rounded capsules dehiscing at the top have seeds of the samaroid type, but quite small. The trees are perhaps most abundant on river banks, but occur also in open country. The seeds readily float and are dispersed by the river when the trees grow on the banks. The species are found in India, China, Malay Peninsula, Siam, Java, Papua, Philippines and Australia, and endemic species occur in the Andaman Islands and on Pulau Condor, off the Siamese coast. It is possible that they reached some of these spots by sea, but they are absent from other oceanic or distant islands.

The Brazilian trees *Sickingia* (*Rubiaceae*) have also globose capsules 1 to 3 inches long, which are 4-celled and split at the top into 2 rounded valves, emitting curved samaroid seeds about ½ inch long and ¼ inch wide.

Seeds Winged by the Funicle (Reversed Samaroid).

The shrub *Pileostegia viburnoides* (*Saxifragaceae*), of the Himalayas, has very peculiar fruits, which are small and globose. The capsule is 4- or 5-celled, with numerous ovules suspended from the top of the loculi. There is a short distinct funicle, below which is a linear oblong pendent wing with a seed at the tip. This wing appears to me to be a part of the funicle, but Hooker seems to consider it an elongated portion of the testa. The seed thus, though samaroid, is a reversed samara, unlike the seed of *Cedrela*, etc., where the wing is formed of the upper edge of the testa. There are 2 species of the genus, the other being Formosan (Pl. IX, fig. 7).

Seeds Winged with a Circular Wing.

In these the testa is expanded into a pair of lateral wings, or they are continued all round, so that the seed is in the centre of the wing. Oblong or elliptic winged seed have been mentioned as frequently passing into terminal wings of greater or less length in proportion to the nucleus, but it is carried to a greater development in the form of a circular wing, quite surrounding the seed, which is usually flattened and frequently continued in a rounded or ovoid capsule. It is not a rare addition to a seed in herbaceous plants, as in *Linaria vulgaris* and *Spergularia*. It occurs, too, in climbing plants, such as *Coptosapelta* (*Rubiaceae*), in which the capsule is round and split into 2 valves,

emitting a number of small round flat seeds fringed with a circular lacerate wing. These Malayan climbers (sometimes of very considerable length) ascend to the tops of lofty trees in the dense forests and along the edges of woods. The most characteristic order of wing-seeded plants, however, is that of the *Bignoniaceae*, the greater number of which possess seeds surrounded by a large thin papery wing, often no thicker than tissue-paper and just as transparent. The greater number of these plants, both climbers and trees, are natives of Brazil. They possess pods which often split gradually into 2 valves, containing a large number of these winged seeds, which, with the wings, are 1 inch or more across. In those which have elliptic or ovoid flattened pods, the seed (nucleus) is usually entirely surrounded by the wing. In those with long narrow pods the seed is often winged at both sides only, *Bignonia*, etc.; but this is not always the case, as in *Oroxylum indicum*, which has gigantic sword-like pods 3 feet long, the seeds are surrounded by a circular wing, and there are other cases similar to this.

As has been stated, far the larger number of *Bignoniaceae* are natives of tropical South America, but there are genera occurring in Africa and tropical Asia. The herbaceous genera *Rehmannia* has cylindrical pods splitting on one side only, containing seeds winged on both sides, and *Amphicosme*, of India and China, with similar pods, has the seeds armed with long silky hairs at each end.

The distance that these seeds can fly on the wind is treated of in the section (p. 129) dealing with that subject, where attention is called to the fact that *Tecoma roseo-alba*, the seeds of which (at present unknown) are probably circular-winged, is the only winged seed plant known to have reached an oceanic island, Fernando de Noronha. It is certain that at least some of these winged seeds are distributed to some extent by water. *Oroxylon indicum*, a slender tree of India and the Malay Peninsula, frequently grows in damp spots along the edge of river banks, and I have seen the seeds drifting about in the Pahang River and continuing their migrations in this way, and it is probable that this takes place in many other of these Bignoniaceous plants. Of *Dolichandrone* (Pl. IX, fig. 11), which has wings at each end of the seed, the wings have become converted into corky floats in *D. Rheedii*, and the plant is thus disseminated by water and wind, as described under Water Dispersal on p. 308.

In these plants, as in the wing-seeded *Cucurbitaceae*, we find examples of seeds winged at both ends, from the sides, forming 2 wings, or completely surrounding the seed, the lateral wings meeting round the top and bottom of the seed. All this class of seeds with papery, almost fragile wings are very much lighter than the stiff samaroid-winged seeds as those of *Gordonia*, *Cedrela*, etc., and float horizontally in the air, not rotating, consequently they may be further disseminated. In the wing-seeded *Cucurbitaceae* the seeds much resemble those of *Bignoniaceae*, but the capsules are of thin, not woody texture, and do not dehisce for their whole length, but only open at the top. They are obconic tubular, or in *Macrozanonia* large, urn-shaped ones, opening by valves at the top. They hang mouth downwards, and when dehisced release the light butterfly-like seeds gradually, as they sway on the long pendent branches of the trees on which they climb.

The wings in this group, often as thin as tissue-paper, are developed laterally or terminally, according to the shape of the capsule. In *Alsomitra*, of Indo-Malaya, Australia and America, the wing is terminal only, and the capsule is elongated, club-shaped and truncate at the top, where it dehisces into 3 valves (Pl. IX, figs. 5 and 6). In *Siolmata*, of Paraguay, the wing projects at both ends; in *Zanonia* it quite surrounds the seed (Pl. IX, fig. 8); while in *Macrozanonia* the wings are lateral, broad at the base, and narrowed to the tips.

These, packed in a large coriaceous but brittle urn, dehiscing at the top, drift out a few at a time, and float in the air to considerable distances, like a swarm of large white butterflies (Pl. IX, fig. 9).

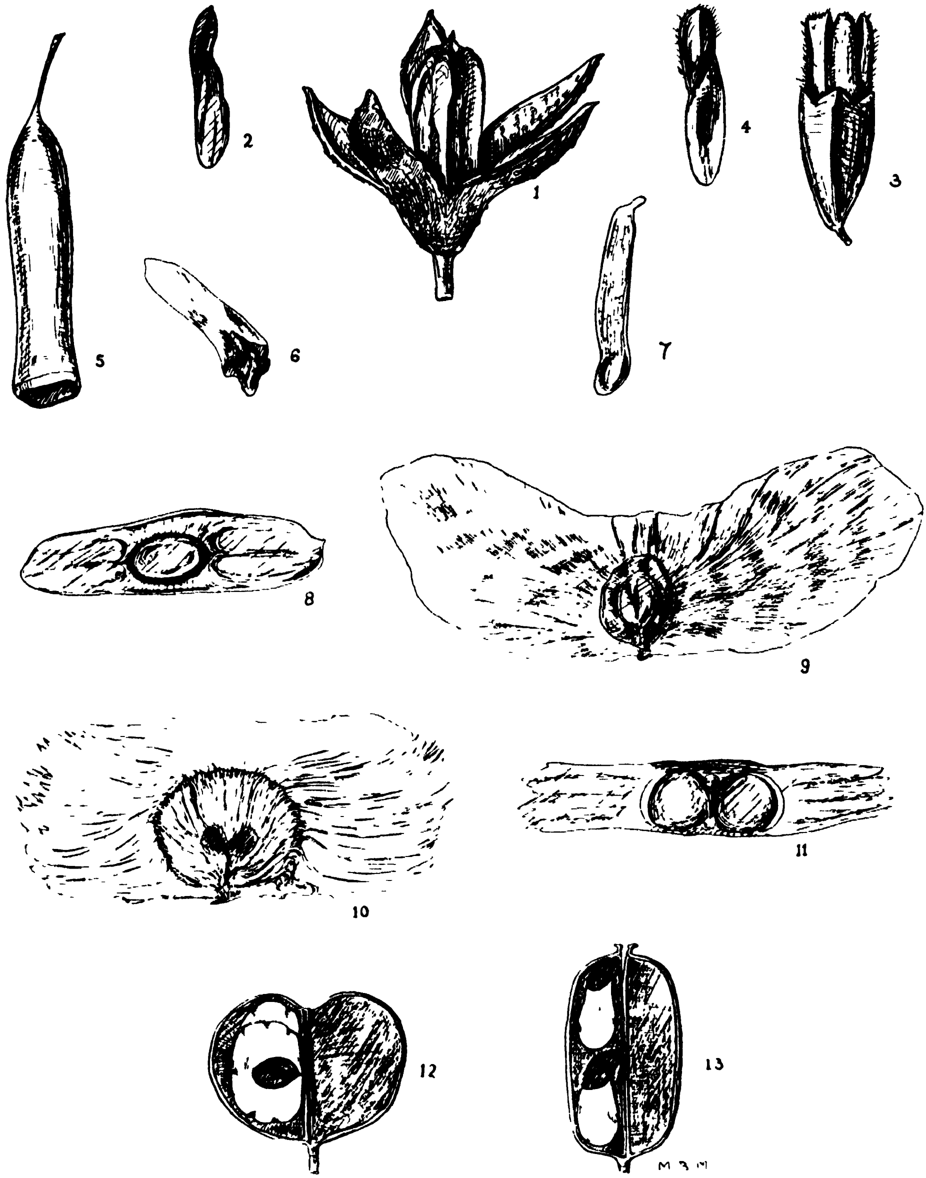
Dioscorea (*Dioscoreaceae*) (the Yams) also have winged seeds; those species with oblong capsules have them winged at one end or the other, but those with rounded capsules have seeds with a very thin, circular wing. These capsules are trilobed, each lobe containing 1 seed and dehiscing along the edge. Most species of Yam possess this form of capsule and seed. The plants are climbers (with very few exceptions) which scramble on small trees and bushes; the long slender racemes of female flowers and fruit hang down and sway about in the wind, and on dehiscence of the fruit, the light seeds flutter away. The species are very numerous and abundant in the tropics in small woods, the edges of forests and in open country. They are found in tropical and subtropical regions of Africa, Asia, America, with a few in Australia. Some even reach temperate regions, such as North America, China and Japan. Except for cultivated species carried about by man, they are absent from Polynesia and also New Zealand, and from oceanic islands. One species (unidentified) contrived to reach Krakatau, but perhaps this was *D. bulbifera*, the bulbils of which can float and may have been brought by sea (Pl. IX, figs. 12 and 13).

Besides trees, shrubs and woody climbers, there are a number of herbs in which the seed is aided in its flight by a wing, an evolution of the testa. *Heliamphora* (*Sarraceniaceae*) has a capsule full of small seeds surrounded by a circular thin wing. In the allied genera *Sarracenia* and *Darlingtonia* the testa is slightly enlarged, but hardly wing-like in any species. These latter grow in swamps in great abundance in North America, and the seeds are probably water-dispersed, as the dilatation of the testa is not sufficient to aid in flight by wind. *Heliamphora*, in which the wing is quite large enough to aid in flight, is an extremely local plant, growing only (so far as is known) on the summit of Mount Roraima in Guiana.

The curious leafless saprophytic Orchids *Galeola*, of East Asia and Australia, also have wings surrounding the seed, but more irregular in outline than the circular one of *Heliamphora*, but, like those, the margin is toothed (*see* Pl. III, figs. 4, 5). These plants have long dehiscent pods with abundance of seeds, and are widely spread, but the seeds are less light than those of other Orchids, and they are absent from all oceanic islands. Something after the manner of the seeds of these plants are the very curious minute seeds of *Pterospora andromedea* (*Monotropeae*). This parasitic plant of California has a tall (2 to 3 feet) lax spike of nodding flowers, after the style of a *Pyrola*. The globose, pendulous capsules, ½ inch long, contain a number of small ribbed seeds, bearing on the top a shortly-stalked crest of thin reticulate tissue. The plant inhabits Pine woods, where its light seeds, with their fine crest-wing, can be drifted along readily by the breezes (Pl. III, fig. 2).

In the greater number of the Gentians (*Gentiana*) the minute and innumerable seeds of the capsule are not winged at all. They are very light and can, like many minute seeds, be dispersed by wind and rain-wash. But some often taller species have distinctly winged seeds. *G. Kurroo*, of the Indian mountains, has linear seeds prolonged at both ends and dilated in the middle. They can hardly be said to be distinctly winged. *G. Andrewsii*, a tall Himalayan species, has the testa of the seed prolonged at both ends and quite thin; the testa is widest at the base, narrowing towards the tip, differing mainly from the seed of *G. Kurroo* in the prolongation of the testa, being thinner, so that the whole seed is lighter. *G. simplex*, of California, has a curved oblong lanceolate seed, the embryo being central and surrounded by a thin testa, and in *G. lutea*, of Europe, and some other species, the testa forms a thin circular wing with

PLATE IX.



WIND-DISPERSAL. WINGED SEED.

FIG. 1.—*Cedrela odorata* (capsule dehiscing).
,, 2.— ,, ,, (seed).
,, 3.—*Glossocarya mollis* (fruit).
,, 4.— ,, ,, (seed).
,, 5.—*Alsomitra integrifolia* (fruit).
,, 6.— ,, ,, (seed).
,, 7.—*Pileostegia viburnoides* (seed, after Hooker).
,, 8.—*Zanonia indica*.
,, 9.—*Macrozanonia macrocarpa* (seed, reduced).
,, 10.—*Oroxylum indicum*.
,, 11.—*Dolichandrone crispa*.
,, 12.—*Dioscorea caucasica* (fruit with seed).
,, 13.—*D. triphylla* (fruit with seed).

[*To face p.* 124

the embryo in the centre. Thus there is a considerable variation in the form of the seed and its testa, in the genus. The Gentians, many of which are very small plants, are extraordinarily widely distributed. Mostly occurring in high mountains, though some (*G. pneumonanthe*) in lowland open country, they seem to be quite absent from islands, and I think it is clear that, light as their seeds are, they cannot be carried to very great distances by wind. It is true that, being largely high mountain plants, they are less likely to be found in islands, as the distance for transport would be very large, but they might well travel by air from one mountain range to another.

Linaria vulgaris (*Scrophulariaceae*), the common English Toad Flax, furnishes a good example of winged seed in herbaceous plants. The whole plant is about 2 feet tall, with a terminal raceme of erect, short-stalked, rounded oblong capsules nearly ½ inch long, which dehisce more or less irregularly by 2 pores, 1 in each cell, at the top, and letting out the seeds a few at a time. There are about 110 seeds in the capsule, and about 20 capsules in a raceme. The seeds are 2 mm. across, the nucleus rounded and papillose on both sides, the wing circular, coriaceous, the edges undulate or lobed, finely striate. They are light and easily blown by wind along the ground in a horizontal position, and float in water. A light puff of wind throws them about 3 feet along the ground, but of course a strong wind or continuous blasts will carry them further. The plant grows on open banks, roadsides, and such spots, and it is much the most abundant species of the genus in England, and, except for one or two cornfield weeds, it is the most common species in Europe. Besides occurring in Europe, it ranges across temperate Asia to China, and is found in North Africa and North America, and has been met with in Japan, Jamaica and Chili, but in these latter localities it has been certainly introduced accidentally by man. It is absent from the Canaries, Madeira and the Azores. I was struck by the abundance of this plant on the disused railway line between Turnham Green and Ravenscourt Park stations, where a flora has appeared consisting almost exclusively of wind-dispersed plants, *Compositae* with plumed seed, *Achillea*, *Epilobium*, *Betula*, *Acer pseudoplatanus*, and some grasses. I do not know of the plant occurring anywhere else in the neighbourhood, which is now covered with houses, but it may be a relic of times when the district was still in the country. I have not seen any evidence of its dispersal by water, although it floats. As it is an inhabitant of dry spots, its seeds are not likely to derive any advantage from being drifted along wet river banks. In most of the *Linarias* the seeds are not winged but angular, often papillose or scrobiculate, but *Linaria alpina*, of the mountains of South Europe, *L. simplex*, *L. Pelisseriana*, tall slender plants of open country in Europe, have seeds similar to those of *L. vulgaris*. To a certain extent *L. vulgaris* seems to owe its wide distribution to human agency, as do so many of the cornfield *Linarias*, but certainly its extreme abundance in Europe is mainly due to its winged seeds.

The small genus of *Caryophyllaceae Spergularia* (*Lepigonum*) is interesting as showing the evolution of the circular wing surrounding the seed. In *S. neglecta* most of the very minute seeds have only a raised rib running round them, but some in the lower part of the capsule have this developed into a thin, distinct circular wing, and in *S. marginata* all the seeds possess a well-marked thin circular wing. These little prostrate plants inhabit saline mud by the sea, and as the seeds are very minute and the capsule lies low on the ground, I do not think that the wing is likely to be of much use as a flight organ, but probably more useful as a floating organ. However, Guppy states that *Spergularia rubra* seeds, with or without wings, do not float (he includes all the now separated species of the plant under the head *Spergularia rubra*), and states that Thuret confirms this. It is interesting to note that *S. rubra*, an

inhabitant of more or less sandy fields, and *S. rupestris*, a sea-rock plant, do not possess winged seeds.

The story of these plants seems to show how very easily a seed may become winged, while the evolution of a distinct wing on the seed may make a vast difference to the whole distribution of the species. A seed of this type of plant that is wingless must owe most of its dispersal to rain-wash, which is a much slower method of dissemination than that of a wind-dispersal mechanism.

In many of the *Liliaceae* with capsular fruits the seeds are more or less flattened, and when discharged by the opening of the capsule at the top and the shaking by the wind, they can be distributed to a short distance. In *Lilium*, however, the thin flat seed is distinctly winged all round by the expanded testa. In *Lilium croceum* the whole plant above ground has withered by the time the fruit is ripe. The stem remains, bearing the many-seeded capsule, open only at the top. As the wind strikes the stem it shakes it violently enough to throw the seeds, a few at a time, fluttering away for a few yards. The seed is nearly ¼ inch long and nearly as wide, elliptic and very thin, the wing surrounding it about 2 mm. wide all round. The *Liliums* are widely scattered, chiefly in mountain regions all over the north temperate region and down as far as the Nilgherries, Burma and the Philippines.

A very similar method of dispersal is found in the *Gladioli* of the plains of South Africa, the erect capsule dehiscing at the top and throwing the thin flat seeds out in the same way. In such cases as these I have little doubt that the seeds can be blown further along the ground when they first settle, but I have not been actually able to see this.

Seeds Winged at the Ends.

In a very large number of plants, where the seeds in capsules or pods are small, they are more or less linear and usually pointed at each end. Such seeds are those of *Deutzia* (*Saxifragaceae*).

The next stage of evolution is the form in which the pointed testa is drawn out at both ends to a long, almost hair-like point, narrower than the central seed. We have all stages of narrowing of the point, from a broad base to an acute point, as in *Norrisia* (*Loganiaceae*), to the finely drawn-out, long, hair-like process at each end, as in *Uncaria* (*Rubiaceae*), *Ledum palustre* (*Ericaceae*) and *Buddleia* (*Loganiaceae*), and even more exaggerated, so as to resemble a solitary hair, as in *Aeschynanthus*.

In the section of the *Rubiaceae* known as the *Naucleae* we have examples of all stages of wing evolution. The flowers of these plants are comparatively small and are crowded into heads. In some of these, *Cephalanthus*, *Sarcocephalus* and *Breonia*, the calyces of the flowers are so compacted together that the whole head forms a fleshy syncarp, and the separate fruits do not dehisce. These plants owe their dispersal to birds or bats, which devour the fleshy mass and evacuate the seeds. In these the seeds, though often flattened, are not winged.

In *Adina cordifolia*, a fairly large tree of India, the capsules do dehisce, not being adnate to each other, as in the last-mentioned set. The seeds are flattened, somewhat elliptic in outline, but pointed at each end. Of this plant Troup states that the seeds are distributed by wind, also largely by water, rains and floods drifting them to the bases of trees, termites' nests, embankments and ditches. The plant is sometimes, he says, epiphytic, showing that wind plays a part in its dispersal. The seeds of *Stephegyne* and *Nauclea*, also

fairly large trees, are similar. All are very small and light, about 300,000 to an ounce.

Hymenodictyon has also small seeds of a similar shape, with, however, the base lobed and the edges denticulate. It is a fairly large Indian tree, and the seeds are distributed to a long distance by wind, according to Troup. This lobing of the base of the seed occurs in other winged seeds of small size, as in some of the *Uncarias* (Pl. III, figs. 11 and 12).

The Gambirs (*Uncaria*) possess the flowers in heads, but quite separate from each other, and often pedicelled. The fruit is a capsule, long and narrow, splitting down the side, but the valves are not freed at either end, so that the seeds escape laterally. They are extremely light, and are furnished with a very long tail at each end, transparent and hair-like, the basal tail often split. The plants (which belong to the section *Naucleae* of the *Rubiaceae*) are long woody climbers occuring on the edges of forests in India, the Malay Peninsula and islands—where they attain their greatest development—to Australia, with 1 species in Africa and 2 in South America. Though their seeds are almost as light as the dust seeds of Orchids, they are quite absent from oceanic or distant islands, and also from Polynesia (Pl. III, fig. 11).

The same class of evolution is found in the *Rhododendrons*, the distribution of which is extraordinarily wide. They range from Europe, through Asia, to China, and southwards through Burma to the Malay Peninsula and islands, and through North America. They are all trees or low shrubs, and in some cases epiphytic. Most abundant in the hilly open country of China and Yunnan, they also occur occasionally in forests, but here they are usually epiphytic. The capsule is cylindrical in shape, splitting into 4 or 5 woody valves from the top, and spreading widely, so that the seeds fly readily on the wing over the open hillsides. The seeds are thin, light and flat, winged usually all round, elliptic and pointed, or oblong and rounded. The terrestrial species R. *orion*, of the Malay mountains, has seeds with the wing pointed at each end, lanceolate in outline, and 2 mm. in length. In R. *grande* the wing is broader and toothed on the edge; R. *arboreum*, of India, has a small oblong seed with the ends tufted with hair-like processes, and R. *ponticum* is very similar. Its seeds are 1 mm. long, oblong, narrowed to the tip, bearing at the upper end a tuft of quite short transparent hairs, and a few longer hairs at the base. The hairs are minutely dotted, but do not appear to excrete mucilage when wetted. The body of the seed is finely longitudinally striate. In R. (*Azalea*) *molle* the seed is shorter and broader, oblong, blunt at both ends, but only the upper one bears the hair-like processes. It is possible that these processes serve somehow to attach the seed to wet soil, but I do not see any further use in them, as they are really too short to act as flying organs or to lighten the seed in any way. All these *Rhododendrons* are terrestrial trees or shrubs inhabiting the open plains and mountain slopes of the north temperate region, ranging down along the mountain chains of India and Malaya (Pl. III, figs. 1 and 6).

The section *Vireya* includes a number of Malayan and Javanese species, mostly epiphytic. R. *Teysmanni*, a shrub which grows on trees in the Malay Peninsula and adjacent islands, has seeds much resembling those of an *Aeschynanthus*. They are very small, elliptic, with long slender transparent tails at each end, the whole seed with its tail being 1 cm. (½ inch) long. It is no doubt that by these slender tails these light wind-borne seeds are attached to the branches of the trees on which they grow. They seem to be evolutions of the slender hairs on the seeds of the terrestrial *Rhododendrons*. It is rather interesting to note that while in the terrestrial *Rhododendrons* the capsule opens at the top, in the epiphytic *Vireya* it opens at the base, so that the seeds in the latter fall downwards to start their flight from branch to branch in the forest, while those of the terrestrial *Rhododendrons*, dispersed from the opening top of

the capsule, are blown horizontally or vertically upwards. I have noted a similar case in the position of the capsules in epiphytic and terrestrial Orchids respectively. I may mention that the seeds of the greater number of the *Vireya* section of the tropical Asiatic species of the *Rhododendron* are as yet unknown.

Nepenthes (*Nepenthaceae*), the Pitcher plants, are woody climbers of no great length, climbing up small trees or bushes, with racemes or panicles of erect capsules dehiscing from the top into 4 (rarely 3) valves. The seeds are narrow, the testa drawn out at each end into long tails, and are very light, resembling the seeds of *Uncaria* (Pl. III, figs. 7 and 11). Macfarlane states that he found 191 and 200 seeds in 2 capsules of *N. alata*, 197 and 167 in 2 of *N. melamphora*, and 456 in 1 of *N. Khasyana*, and remarks that their extreme lightness and relatively large exposure to wind favours wind-dispersal to a large degree. The centre of distribution seems to be the mountain range of Kinabalu, in Borneo, from which they appear to have radiated in all directions. They are abundant in the Malay Peninsula, Sumatra and the islands, to New Guinea and the Philippines, and are found in North Australia. A few occur in Cochin China and Siam, and 1 in the Himalayas, 1 in Ceylon, 1 in Madagascar, and 1 in the Seychelles. These latter two have seeds only shortly tailed. There is some suggestion that these seeds may have been borne to the more remote localities directly by wind, but I do not think it possible that seeds could have flown, say, from North Sumatra to Ceylon, or Ceylon to the Seychelles. Light as they are, they are by no means as light as seeds of Orchids or Fern spores. The weight of the seed of *N. phyllamphora* is given as ·000035 gramme, while that of *Dendrobium attenuatum* is .00000565 gramme, so that the seeds of the Pitcher plant are about 300 times as heavy.

The fact that *Nepenthes* is absent from distant islands seems to show that it cannot fly to the great distances that Orchids do. In the Malay Peninsula, and I think also in Borneo, *Nepenthes* is found in lowland country near the sea, and on the summits of high mountains, but not in the densely forested areas, lowland and mountain, up to 5,000 feet altitude. In open forest on mountain tops they do occur at a lower elevation, e.g., Penang Hill, 2,500 feet, and Mount Ophir, 5,000 feet, altitude. There are several other plants which have the same distribution, e.g., *Baeckia* (*Myrtaceae*), *Leucopogon* (*Epacrideae*), *Dianella* (*Liliaceae*), *Gahnia tristis* (*Cyperaceae*), all of which have a different system of dispersal, and I have reason to surmise that these, with *Nepenthes*, are portions of a long-past flora which occupied the whole of the Malay Peninsula before the later rain-forest region overwhelmed it. We have Malay genera in Ceylon, such as *Acrotrema*, *Dipterocarpeae*, etc., which could not possibly have passed between these countries except by land, and we have signs also of a connection between Ceylon and the African region in the tall *Lobelias* and *Engleranthus* (*Labiatae*), evidencing a land connection between these two countries at some period, and it may be that *Nepenthes* passed over to its most distant points, without having to cross any large extent of sea, in the periods when there was a land connection between these distant and now isolated spots. The lighter-seeded *Aeschynanthus* and *Rhododendron* are found in Ceylon, but not in the Seychelles. There is no doubt, however, that both of these came southward from North India and not from the Malay region, as the affinities of the species show.

Buddleia (*Loganiaceae*).—These are shrubs or treelets, one at least (*B. asiatica*) being sometimes a herb, in which the capsules are borne usually in long dense racemes. In *B. Colvillei* the seeds are quite unprovided with wings, and *B. braziliensis* has simply angled seeds. In *B. sessiliflora* and *B. asiatica* the seeds are surrounded by a wing, which is thin and transparent, so that the shape of the seed and the wing is of a somewhat ellipsoid form. In *B. variabilis*

and its allies the points of the testa are drawn out into an elongated process gradually narrowed to the tip, the terminal one being slightly longer than the basal one. The whole seed is 4 mm. long, the nucleus being only 1 mm. long, oblong and rounded (Pl. III, fig. 9). As *B. asiatica* occurs as a herb in rice fields in the Malay Peninsula, I have very little doubt that the seeds are to some extent dispersed by floating.

Ledum palustre (*Ericaceae*), a low dense shrub of the arctic regions and mountains of Europe, possesses minute seeds with a finely reticulate transparent testa drawn out into long acuminate points, the whole seed being 5 mm. long. The rounded capsules hang downwards on their slender pedicels and dehisce from the base into 5 valves, so that the opening to release the seeds is uppermost. We have already seen that this is usually the case in plants whose seeds are destined to be dispersed by wind, to which they are more fully exposed than if the opening of the fruit were pointing to the ground. There are about 4 species of the genus, ranging from Arctic Europe and America, through the mountain ranges of Southern Europe, and across Siberia to China and Japan. It is easy to see how readily the seeds of this plant can be blown across these plains and mountains by the blasts which sweep across the open country, and how it is that the plant has travelled so much further than the heather *Calluna*, *Kalmia*, and other mountain bushes which have a less apt means of dispersal.

Distance of Flight of Winged Seeds.

(*See also* Table, p. 71.)

The flight of winged seeds is by no means as far as that of plumed seeds, but I have not a large number of observations on their flight.

Dyera costulata (*Apocynaceae*) has flat, round, winged seeds in a pair of follicles, opening along the upper edge. From a tree 80 feet tall in the Singapore Botanic Gardens I found the seeds blown a distance of 40 yards by a fairly strong wind. The tree sometimes attains a height of 200 feet, and I have little doubt that the seeds are often blown to a much greater distance, as the trees in some places are rather sporadic, at considerable distances apart.

Macrozanonia macrocarpa (*Cucurbitaceae*), a climbing plant of Java, Borneo, New Guinea, Aru and the Philippine Islands, has a very large coriaceous obovate capsule over 6 inches across, containing a great number of flattened seeds with lateral wings of the thickness of tissue-paper, the whole shape of the seed and its wings being that of a butterfly, and being 5 or 6 inches across from tip to tip. The capsule opens at the top into curved lobes, and, being pendent, releases slowly these very large and light seeds, which are said (*Kew Bull.*, 1920, p. 127) to have been picked up on the deck of a ship at sea, but at what distance from land is not recorded (Pl. IX, fig. 9).

It is clear that winged seeds do not fly, under the best circumstances, as far as plumed seeds, though they may in many cases be driven further along the ground, in suitable spots, by the wind (as happens also with winged fruits), and, as they are comparatively light, they may, being blown into rivers, be drifted by water a still greater distance. The light round winged seed of *Oroxylon indicum* (*Bignoniaceae*), a river-bank plant, often falls into the river and is probably dispersed along its banks in this way (Pl. IX, fig. 10).

The distances of flight recorded are so short that it would seem highly improbable that any could be carried to distant oceanic islets by wind, and indeed we find, as in the case of winged fruits, that they are rarely to be found in oceanic islands.

The following are the only cases I have met with. In Fernando de Noronha

I found a species of *Bignoniaceous* climber, *Tecoma roseo-alba*. No ripe fruits were found, but it undoubtedly must possess long cylindrical fruits with thin winged, rounded or transversely oblong seeds, with wings as thin as tissue-paper. The species is endemic, but allied to plants on the neighbouring coasts of Brazil. The plant grew only in thickets in the middle of the island, and not on the seashore. However, it is quite possible that it had originally arrived by drifting in the sea to the island.

In Krakatau a species of *Dioscorea*, unidentified, was found in 1919. These plants have thin winged seeds, but it is possible that the species was one of the bulbiliferous kinds (e.g., *D. bulbifera*), and that the bulbils had drifted to the island. *Aristolochia Tagala* was also found. This has flat winged seeds which certainly fly for some distance when blown, but I hardly think it can possibly have been carried by wind from Java, and may perhaps have been sea-drifted on a log or in some such way. *Pinus canariensis* is a native of the Canary Islands, but there is much evidence of the islands having been formerly attached to the mainland (*see* Island Floras p. 680).

These are all the wing-seeded plants I have been able to find recorded for oceanic islands. Like winged fruits, they are very scarce, and their absence seems to show that fruits and seeds dispersed by wings are strictly continental.

Seeds Winged by the Valves of the Capsule.

An unusual form of winged seed is that of *Glossocarya* (*Verbenaceae*), a small genus of about 5 species occurring in India, Ceylon, and Siam, to the north of the Malay Peninsula. The plants are all shrubby climbers with masses of small white flowers. The fruit is a capsule, oblong, blunt, about ½ inch long, and hairy at the tip. This dehisces into 4 valves, each of which contains a small linear oblong seed at the upper end. The valve edges curve over the seed and, becoming completely detached, act as a wing to the seed, so as to drift it away from the parent plant (Pl. IX, figs. 3 and 4).

Summary.

Winged seeds are by no means as abundant as winged fruit, but this is probably due to the wings of the seed being limited to one organ, the testa, while in fruits we have not only the sides of the carpel but also portions of the perianth which can be modified for flying purposes. The limit of distance of flight of winged seeds is much the same as that of winged fruit, though the minute seeds, with the testa dilated, leading up to the dust seed plants, probably fly to a considerably greater distance. Still, this class of plant has not crossed the seas to an oceanic island unless they have also been adapted for sea transport (e.g., *Melochia arborea*), as has been the case in winged fruits (*Casuarina*). Winged seeds may float in river or flood (*see under* River-Dispersal), but apparently the wing is an obstacle in dispersal by rain-wash, as the winged seeds lie flat on the ground after falling. Hence most of the minute seeds of herbaceous plants are not winged.

PLUMED FRUITS AND SEEDS.

Plumed fruits are those which when ripe bear a number of hairs, usually soft and silky, by which they may be drifted by the wind when they are detached from the receptacle, raceme, or panicle. These hairs are not developed, or, at least, not fully developed, till the fruit is ripe. These plumed fruits are always 1-seeded.

Plumed seeds are always contained in a capsule or pod, in which they lie in a compact mass till the pod dehisces, when they expand their plumes and are floated away, a few at a time, to a great distance. In most the hairs are fine, simple, straight and silky, but some have branched hairs, and in some the hairs are curled and form a woolly mass. The principle of dispersal is the same in all these plants.

Plumed fruits and seeds fly much further than winged ones. Some of the lightest ones have been known to travel hundreds of miles. They are usually very light, and can rise and fall on the wind, even rising again from the ground, after having fallen, to a considerable height. In fruits with plumes the flying organ is very variously formed in different groups. In the *Compositae* the plume usually consists of an evolution of the persistent accrescent sepals, terminal on the achene, which is enclosed in the calyx tube.

In some plants, *Pulsatilla*, *Geum*, etc., the plume is formed by a modification of the persistent and accrescent style, which is furnished with long silky hairs.

In many of the small *Amarantaceae* of the seashores and deserts the perianth lobes are covered on the outer or inner face, or both, with silky or curly hairs, and when the utricle with its single-seeded achene is ripe, the dry persistent woolly perianth helps to bear it along over the sand or the mountain-side.

In grasses it is the spikelets or pedicels which bear the soft long hairs, and occasionally an elongated awn is plumed.

In the Cotton Grass (*Eriophorum*) the plume is formed of hypogynous bristles which, surrounding the nut, form by continued growth the white plume by which the fruit is drifted across the moors.

In the Reed Mace (*Typha*) the plume of the minute fruit is formed from long hairs borne on the gynophore (a stalk which supports the ovary).

In the Plane trees (*Platanus*) the long hairs which drift the fruit away are outgrowths from the ovary, and in some of the Anemones the whole achene is covered with soft woolly hairs which act as flight organs.

In plumed seeds the silky hairs are developed usually at the apex or at the base of the seed, and are an outgrowth from the testa. Occasionally they cover the seed completely, and then are often woolly, curly and white, as in the Willows and Cotton trees and bushes. They float away on the breeze as far as do the plume fruits, and rise and fall on the wind in the same way. The hairs of these fruits and seeds, especially when wetted, are adhesive frequently to fur of animals, birds' plumage and the clothes of man, and the plants are often disseminated by them, but this is more of an accidental method of diffusion.

Distance of Flight of Plumed Fruits and Seeds.

The distance to which the plumed seeds and fruits can fly without coming down is often difficult to judge, as they drift away often so fast on a good wind that it is not easy to keep up with them, and in many cases they rise to a considerable height after starting, and are soon lost to sight. During the fruiting season great quantities of thistledown plumes are to be seen drifting along through the air to considerable distances. It will be found, however, that in a large proportion of cases the silky plume has become detached from the fruit, and, being thus much lighter, may drift along for miles before coming to the ground.

When a plumed fruit of a Composite, in its flight, comes up against a branch of a tree or other such obstruction, the achene becomes detached and falls to the ground, while the plume often goes on a long way further. This is why thistles, dandelions, and such plants, are constantly found on the edges of thickets, bases of hedges, mouths of rabbit burrows, and similar spots. It is not, therefore, sufficient to measure the distance to which the thistledown

travels, as a criterion of the speed at which a plant can migrate from place to place, unless the down is still attached to the fertile achene. E. P. Turner records seeing thistledown drifting over the sea 500 miles from land, but could not determine whether it was carrying seeds. The same remark applies to the downy plumes of the Willows and Poplars. One may often see these plumes flying in abundance to a considerable distance from the parent tree, and the ground covered with it like snow, and yet not a seed present, for these trees are unisexual, and if there is no male in the vicinity, the ovules may be unfertilised. In spite of this the capsules dehisce and emit the barren plumes in abundance.

The most reliable method of calculating the migratory power of these plants lies in a careful examination of those that are found in remote islands, which cannot have arrived there by any other method but by wind-carriage, and here caution is necessary, inasmuch as it does happen that (especially when wet) plumed seeds or fruits may become adhesive to birds, and so be conveyed for long distances. I have given an account of the wide-dispersed plumed fruits and seeds at the end of this section. The furthest record I have of long flight is that of *Chevreulia stolonifera*, from South America to Tristan d'Acunha, 5,500 miles, and several *Compositae* of African origin to St. Helena, a distance of 1,140 miles.

Dandeno (in "Parachute Effect of Thistledown," *Science*, 1905, 568) gives an account of the factors in the flight of the plumed seeds of *Carduus arvensis*. He says: When dry the head of the thistle expands—that is, the scales of the involucre spread, and indeed deflex, and expose the fluffy mass of seeds to the air. The down on the receptacle serves the purpose of keeping water from the head, so that the achenes remain thoroughly dry. Dampness tends to hold the achenes to the head, so that the fluff may float away without the achene. The achene and plume, however, are covered with a substance of an oily nature, so that they do not get wet. When the down with its attached achene is exposed to dry air for a few days, the contracting upper end of the achene causes it to rupture from the collar of the calyx-down, and thus eventually separation takes place. This is an advantage, because the seed may thus reach a suitable place for germination. If the pappus were retained, the down would be a hindrance by holding the achene above the soil. The separation would be likely to take place in the air because of the favourable conditions of drying out. The cells of the pappus are filled with air when the achenes are mature, which adds to the buoyancy. The weight of the achenes without the down is 0·108 gramme. So that he calculates that for each gramme weight of achenes there is a surface area of 6·23–5·42 cm. A thistle fruit starting from an elevation of 20 feet would take $\frac{20}{1848}$ hours to fall, and if we suppose the wind to be blowing 20 miles an hour, the achene would be carried 0·21 (or about $\frac{1}{5}$) of a mile.

J. Small (in "The Dispersal of Compositae," *New Phytologist*, 1918, xvii, 200) gives an elaborate account, with figures, of the mechanics of the flight of plumed achenes. He shows that as long as the relative humidity of the air remains above 0·77, and the fruit does not encounter any obstacle, a horizontal wind of 1·97 miles an hour can carry it to any distance. If the air becomes moist, the pappus closes up and the fruit falls rapidly. Praeger and Guppy have calculated the rate of fall of many plumed fruits in quiet air, and show that they require an elevation of 1 mile with a wind of 50 miles an hour before they can go a distance of 50 miles.

Praeger writes (in the "Clare Island Survey"):—"*Epilobium montanum* seed "takes 20 seconds to fall 12 feet. If it is liberated 5 miles away from the "island, with a gale of 50 miles per hour, it would take 6 minutes to reach the "island, but would then fall 216 feet." But the fall is not in nature continuous.

The wind blows in waves. Over land, where sufficiently open, the plumed seed is carried along by the wind-wave till the wind slackens and perhaps ceases; the seed then falls, but the next wave may raise it again and cause it to go further, and this may be continuously repeated till it is stopped by some obstacle, or the plume gets wet and it can rise no more.

Now, very light plumed fruits or seeds, like those of the Dandelion or *Epilobium*, or some of the achenes of the Thistles, when detached, fall slightly at first, often to the ground, along which they may be blown, but if the wind is strong they usually rise to a considerable height on an upward breeze.

I have seen the fruits of the Dandelion, which probably started within 6 inches of the ground, rising to 12 feet or more, and steadily going forward in a straight line at that height in a moderate breeze. The seeds of *Epilobium angustifolium*, starting about 3 feet from the ground, rose 30 or 40 feet, and were then lost to sight, and thistledown rose to a still greater height. There is no reason why such fruits and seeds should not fly like this to very great distances, until they arrive at a spot where the air is too wet or they meet a rainstorm, when they would fall. Naturally the higher the point is from which the fruit starts, the further it will go, and this may have some bearing on the flight of *Chevreulia stolonifera* from the Chilian Andes to Tristan d'Acunha.

In a flight across the sea the matter is different from that across the land, as should the plumed seed reach the water it cannot rise again, so that in order to reach a distant island it is necessary for it to fly at a considerable height on a continuous or nearly continuous gale in tolerably dry air. As these conditions must be comparatively rare, it is not to be wondered at that the occurrence of plumed-seed plants is scarce in distant islands.

Blumea spectabilis, a native of the Malay regions, including Java, is found in Christmas Island, and is the only plumed Composite which is met with there. In the Malay regions it is a plant of about 3 feet tall and inhabits the hill forests at some altitude. Its plumed achenes would have to rise above the trees, usually about from 100 to 150 feet tall, among which it grows. This would be effected by some accidental ascending currents of air. Should a fairly continuous gale of wind be blowing at the time in the direction of the island, it might cross the intervening water (200 miles) in a few hours, and only fall when it reached the damp air arising from the forests of the island, or perhaps a fall of rain on the island might bring it down. If only one of the achenes reached the island, the plant might establish itself there. I have selected this plant as an example of long-distance flight of a plumed achene because it is highly improbable that it could have been conveyed by attachment to a bird. None of the sea-birds could have picked it up on their plumage and brought it over, as they do not frequent the forest ground, and the plant does not grow by the seashore. The only bird of Christmas Island it could have come into contact with is the ground pigeon (*Chalcophaps*). It is certain that some plumed seeds have been carried by birds to distant islands (e.g., *Sonchus oleraceus* to White Island), but it does not appear to be a common condition. Among the plants brought to Krakatau after the eruption were 2 species of *Blumea*, *Erigeron linifolius*, *Emilia sonchifolia*, *Vernonia cinerea* and a *Senecio*, all common plants in the lowlands, *Pluchea indica*, a tidal marsh plant, and *Erecthites*, a South American weed introduced into Asia, with, later, *Gynura sarmentosa* and *Mikania scandens*. All these are common plants in tropical Asia, and many of them now weeds in cultivated land, with short plumes and light achenes.

A plumed achene, such as that of *Hypochaeris*, *Taraxacum* or *Tragopogon*, when it falls to the ground, should it alight on short grass, or a road, or on the leaf of a shrub, lies on its side supported by the projecting hairs of the pappus, and is then carried on further by the next puff of wind, till it reaches either a

hedge or bush, where the achene breaks off from the pappus and falls on a soft open soil-space, and becomes attached to the soil by the short, often hooked, processes of the achene, if the achene is armed with them, as is the case in *Sonchus* and *Taraxacum*, or merely by the hairs covering the achene and pointing forward to the apex, as in many species of *Senecio*, especially those which inhabit dry open country. In the swamp or mud-bank growing species, *Senecio aquaticus*, etc., the achenes are smooth, and in *Sonchus palustris* adapted for floating, so that they drift into the river and are eventually stranded by the fall of the water. In other Composites the hairs are viscid (*Senecio vulgaris*) or armed with short processes (*Helminthia*), and are thus readily arrested in their flight along the ground, or are readily, when wet, attached to the fur of animals and feathers of birds, and thus further disseminated.

It seems tolerably clear, from the study of plume-fruited and plume-seeded plants in distant islands, that the fruits or seeds can fly at a single flight quite 1,000 miles, and even much further, but it is, generally speaking, possible for the plants of this nature to have been brought to an island accidentally attached to the feathers of birds, and this has to be taken into account.

It will be noticed that the plume-fruited *Compositae* are more abundant and widely spread than are the plume-seeded *Apocynaceae* and *Asclepiadaceae*. This I take to be simply brought about by the fact that the latter orders are adapted for tropical or at least warm countries only, while *Compositae* are able to adapt themselves not only to the temperate and cold regions, but largely also to warm and tropical regions. That *Compositae* with plumed fruit are scarce in the rain-forest area is simply due to the dense, often lofty vegetation which they are unable to penetrate. Where the forest is felled and cleared these plants soon appear. Even the tropical *Apocynaceae* and *Asclepiadaceae* are rare, except in the latter order, in the form of epiphytes on the exposed branches of the highest trees.

More plume-seeded fruited plants, *Compositae*, grasses, and *Asclepiads*, reached Krakatau in 23 years (14 species) than have reached and settled in Christmas Island in the whole time of its existence (2 species). Krakatau is about 25 miles from Java, and Christmas Island 194 miles. Allowing for the difference in soil (Christmas Island being mainly coral rock), this suggests that a very large proportion of plumed fruits and seeds blown out to sea by wind from Java southwards drop into the sea and perish before they can travel 194 miles.

We find, however, some plants with plumed fruits and seeds in even remoter islands than Christmas Island. The distance of flight depends on the velocity and continuance of the wind from the mainland, and the dryness of the atmosphere at the time of flight. It is on continental plains that the plume-seeded *Compositae* are most abundant and varied, and the rapidity with which these plants can move across a continent is very great, and certainly accounts for their wide distribution. If one estimates that the plumed achene of an annual Composite flies only 25 miles at a flight, and continues establishing itself at that rate in the same direction for 1,000 years, the plant would have spread in that time 25,000 miles, or completely round the earth.

It is worthy of notice that two of the largest and most widely spread orders of the flowering plants of the world, and those that contain the largest number of species, are both orders of plants mainly depending on their means of dispersal by wind, the *Compositae* and *Orchidaceae*, and, further, that of these wind-dispersed plants, the areas occupied by definite species are comparatively small.

I here exclude temporarily the plants which have had the advantage of being assisted in their travels by man. Indeed, the greater number of very widely distributed species of *Compositae* of the tropics owe their wide range to adhesive organs, by which they are diffused about the world by man and his domestic

animals. Many of them have no adaptations for wind-dispersal, and even if the achenes are plumose, the plumes themselves or the hairs on the body of the fruit serve as adhesive organs when wet. I find the fruits of the Dandelion (*Taraxacum*) adheres readily to cloth by the short processes on the plume hairs, though it has also spines on the upper part of the achene which sometimes cause it to adhere, and the fruits of the Groundsel (*Senecio vulgaris*) have mucilaginous hairs which, when thoroughly wetted, can adhere to cloth, etc. Thus, in the Malay Peninsula, most of the *Compositae* recorded as occurring there are weeds, usually from South America, carried about by man. There are about 46 species, of which 17, occurring in both hemispheres, but widely distributed in Asia, have no plumed pappus; about 6 introduced species have a plumed pappus, and only 2 or 3 occur in both hemispheres; most of the remaining plume-fruited species have probably been introduced by man accidentally, in merchandise or attached to clothes, etc., without aid from the pappus except as an adhesive organ. When a flying plumed achene meets with a bush, tree or any obstacle over which it cannot rise, it falls to the ground. Hence we find these plants usually at the edges of forests, woods or bushes. In the case of Thistles and some other *Compositae*, when the achene touches a bough it becomes detached from the plume, which continues its course. Most of the thistledown we see so abundantly in the autumn floating along is already freed of the achene. On the Dorsetshire downs I observed that, while in and around gorse and other bushes the plants which came up were mostly bird-borne, where a gorse bush had been burnt till only the stem and branches remained, the ground beneath and around it bore abundance of thistles (*Carduus pycnocephalus*) and *Sonchus oleraceus* and nothing else, though the latter plant hardly occurred elsewhere on the downs, the achenes having doubtless been blown from the lowlands below. In these skeletons of bushes the birds naturally did not roost and deposit seeds, but the spaces between the burnt branches were wide enough to allow the plumed achene to pass through, and many so doing struck the branches and the achene fell to the ground and grew.

Plants with plumed fruits are characteristic of open countries, steppes, moorland, and river banks, and the same may be said of plants with plumed seeds. Except the epiphytes, they are almost completely absent from forests, only a few occurring on the edges and a few big trees (*Alstonia*, etc.) which occur in the lowland forests. They are also scarce in high wet mountains. They are abundant on river banks because of the constant up-and-down-stream breezes which readily disperse the seeds. Even the epiphytic *Asclepiadaceae* and *Cyrtandraceae* are not very abundant in forests, and usually occur on the highest parts of the trees exposed to the wind. They are more readily scattered as individuals than plants with no special adaptation for dispersal, or even than plants with winged fruit. Thus one may often find patches of ground covered with *Capsella*, *Digitalis*, or *Scilla*, to the exclusion of everything else, and often consisting of many dozens or hundreds of individuals. Such a collection of plants of one species is rarely to be seen in plants with plumed fruits or seeds, except in the case of those with copious rhizomes, such as *Imperata* (Lalang grass), *Hieracium aurantiacum*, or some of the Thistles, the apparent masses of individuals in these cases being really only from one or two seedlings propagating by rhizomes. One may contrast the spread of Daisies (*Bellis perennis*), in which the achenes are not plumed, with the Dandelion. The Daisies are found in great plenty together, the leaves of the different individuals often touching, while the Dandelions are usually at least 3 feet apart. Thus, though Daisies and such plants are abundant in patches, Dandelions are scattered in every corner of roadsides, waste ground, etc., where they can grow. The same scattering of plants can be seen on hillsides and meadows where *Senecio*

Jacobaea grows. The individual plants are mainly isolated. In Dandelion and Groundsel the plumed fruits when detached often fall to the ground by the side of the plant, if the wind is not strong, but then they are prevented from actually touching the ground in many cases by the plumes, and lie on their sides till another puff of wind lifts them and carries them along. Sometimes the wind will lift a fallen or falling fruit high into the air, and it soars higher and higher till it gets carried a long distance. This is particularly conspicuous in the case of the seeds of *Epilobium*.

Fall of Seeds in Still Air.

Praeger (in the "Clare Island Survey") gives an extensive list of the rapidity of fall of seeds and achenes in still air. In the matter of dispersal this is important because of the possibility of transport by wind, even in the case of small seeds not plumed or winged. For the slower they fall the further they can go if there is a breeze blowing, and this, in tall plants especially, may be enough to carry them a sufficient distance from the parent plant.

The following list gives the time taken to fall 12 feet in the given number of seconds. I sort them according to slowness of fall :—

Plumed Fruits and Seeds.

Typha latifolia	falls 12 feet in	34·0	seconds.
Epilobium palustre	,, ,,	23·0	,,
Salix repens	,, ,,	22·6	,,
Epilobium montanum	,, ,,	20·0	,,
,, *hirsutum*	,, ,,	19·0	,,
Salix aurita	,, ,,	19·4	,,
Senecio sylvaticus	,, ,,	17·3	,,
Lactuca virosa	,, ,,	16·4	,,
Eriophorum angustifolium	,, ,,	16·2	,,
Eupatorium cannabinum	,, ,,	16·0	,,
Salix pentandra	,, ,,	15·2	,,
Carduus arvensis	,, ,,	14·0	,,
Inula salicina	,, ,,	13·3	,,
Senecio vulgaris	,, ,,	12·8	,,
Cnicus lanceolatus	,, ,,	12·4	,,
Sonchus oleraceus	,, ,,	12·7	,,
Hypochaeris radicata	,, ,,	11·3	,,
Senecio Jacobaea	,, ,,	10·0	,,
Pulicaria dysenterica	,, ,,	10·0	,,
Taraxacum dens-leonis	,, ,,	8·5	,,

The remainder in the list, including *Tragopogon*, *Crepis*, *Leontodon*, *Erigeron acre*, *Carduus pycnocephalus*, *Inula crithmoides*, all fall 12 feet in from 3 to 8 seconds, and *Armeria* in 1·4 second.

Winged Seeds.

Pinus sylvestris	falls 12 feet in	6·7	seconds.
Narthecium ossifragum	,, ,,	6·0	,,

The rest recorded from 1·5 to 3 seconds.

Dust Seeds.

Epipactis palustris	falls 12 feet in	22	seconds.
Orchis incarnata	,, ,,	12	,,
Habenaria conopsea	,, ,,	12	,,

Ordinary small seeds without any mechanism for dispersal fell 12 feet in from 1·5 to 5·5 seconds.

PLUMED FRUITS.

Plumed Bracts (Glumes) and Pedicels.

Plumed Grasses.—The greater number of grasses appear to have their fruit dispersed by wind to a large extent, but many have no more flying apparatus than is formed by the light uppermost glume and palea, which enclose the grain as in a closed boat, the glume, being wider than the grain and very light, acting as a wing as described under the section dealing with Glume Wings (p. 99). But to this is added, in many grasses, a better flying mechanism in the form of silky plume-like hairs, which are attached either to the glume itself, or form a circle round the base of the spikelet, and, being much longer than the glume, can readily support glume and fruit in the air, so that they may be borne to a great distance by the wind. In most of these grasses the panicle or spike is tall and stands up well above the foliage, as in *Saccharum*, *Gynerium*, etc. In some cases the awns themselves form flying organs, being light and long, and in some plants, e.g., *Stipa*, the awn itself is plumed.

In most of the plumed grasses the glume and grain are reduced to a very small size and are very light, so as to be easily transported.

Widely as the plumed grasses are dispersed over continental areas, it is remarkable how rare they are in oceanic islands, though other grasses with apparently much less facility for travel are often present.

In the island of Krakatau, 25 miles from Java, 5 species had appeared by 1897, 14 years after the destruction of the vegetation by the volcanic eruption. These were *Phragmites communis* and *Pennisetum macrostachyum* (*Gymnothrix elegans*), which had arrived by 1886, only 3 years after the eruption, *Imperata arundinacea*, *Pogonatherum crinitum*, *Saccharum spontaneum* by 1897. Up to 1919 no more plumed grasses had appeared except *Oplismenus compositus*, which perhaps was more probably brought as an adhesive fruit. All the grasses above-mentioned are widely distributed over tropical Asia, except the rather local *Pennisetum*. The rapid appearance of the common Reed (*Phragmites*) is to be noticed in view of its very wide distribution.

In Christmas Island is one plumed grass, *Ischaemum nativitatis*, endemic but allied to some Polynesian species. Its plumed spikelets, or rather joints of the spike, were certainly dispersed about the island by wind, and I have recorded how I found them blown into little piles in the holes in the coral rocks by the wind; but the spikelets seem to be too heavy to be transported thus to any distance over sea, and I suspect it was introduced by adhesion to the feathers of some bird.

Many grasses occur on oceanic islands, but in these cases they are not plumed, and though they may be disseminated locally by wind, they evidently cannot cross the sea. They seem mostly to have been brought by adhesion to birds' feathers or on their feet, or in some cases by sea-drift.

Phragmites communis (the common Reed).—In the heads of this tall grass the spikelet is somewhat elongate, so that the upper flowers are borne on a slender rachilla which is covered with long silky hairs (Pl. XI, fig. 3). The glumes are usually quite glabrous, and the fruiting spikelet breaks off above the two lower glumes. The Reed possesses a rhizome, so that it often occurs in great masses. It varies but little. The common Indian form, which has been separated under the name of *Ph. Roxburghii*, has distinctly smaller spikelets. The panicle is often very large and contains a vast number of spikelets. The whole plant varies in height from 2 to 10 feet tall, according to locality.

The Reed grows rapidly and abundantly on river banks, marshes and pools

all over the whole world with the exception of Polynesia and New Zealand, but is absent from oceanic islands, which, however, do not usually contain spots suited for its growth. It is, in fact, the most widely distributed species of all flowering plants in the world. This is not merely due to its adaptation for dispersal by the wind, but to its adaptability to climate. It is able to thrive in the cold of Finland, 69·40° N., as well as it can in the heat of the equator. It is, however, most abundant in the north temperate regions of the Old World, and is less common in America, though it occurs as far south as Chile. It is, also, occasionally planted in Argentina for stable litter. It can grow on seashores, on clay or wet sand, at sea-level or up to 10,000 feet altitude in Thibet. Its flight distance does not seem to be very great, as we have no record of it from any very distant island, but it was one of the first 7 grasses to reach Krakatau, after the destruction of the vegetation by the volcano, from Sumatra or Java, a distance of from 23 to 25 miles away, and it is met with in Tasmania and New Caledonia. It is possible that in some cases the seeds of the Reed may have been transported by attachment to birds nesting among the reeds, but as the spikelets can evidently fly 25 miles without falling, this would be a very secondary method of dispersal.

Imperata is a genus of about 4 species, with close, usually spicate panicles, dense and white with silky hairs. These silky hairs are developed at the base of the spikelet, and are much longer than it, for the spikelet is very short. There are 2 species in the Old World, *I. cylindrica* and *I. exaltata*, and 2 closely allied ones, *I. braziliensis* and *I. caudata*, in the New World (Pl. XI, fig. 1).

I. cylindrica is very widely distributed, and in open country in the tropics extremely abundant, covering large areas, where it usually flowers and fruits after being burnt. It owes its abundance mainly to its underground rhizomes, which are usually so deep beneath the ground that the fire which destroys the foliage does not affect them. Any fragment of the rhizome will grow. Owing to its great abundance, it is used for packing material and litter, and cattle fed on it pass the seeds unharmed. These methods of dispersal undoubtedly account to some extent for its distribution in many places, but it spreads largely also by its plumed spikelets. It occurs on the Mediterranean seashores, in Syria, Egypt, the Canaries, India, China and Formosa, Japan, the Malay region, Australia (1802), New Zealand (1817), Sunday Island, Kermadec, tropical Africa, Comoro Islands and Madagascar. It is remarkably absent from all oceanic islands, but had reached Krakatau by 1897. I found in Singapore that in a fairly strong breeze its spikelets only flew 16 yards when started at about its ordinary height, 2 feet or so from the ground. Further, I found that it could not cross a comparatively short barrier of forest, say, 30 yards. If a clearing is made in forest, the plant does not appear unless a wide open path is made through which it can come. This strongly suggests that in the localities in the Canary Islands and Kermadec group where it occurs, it was carried accidentally by man. There seems no doubt that it can grow in open spaces almost anywhere where it is warm enough for it, though it quickly perishes in the shade. I have even seen it growing in thick sulphurous smoke at Kawa Manuk and Papandayan volcanos in Java, where little else would grow.

Contrasted with this plant is the behaviour of *I. exaltata*, rather a taller plant, but not producing the great abundance of rhizomes which *I. cylindrica* does. It is only shortly rhizomatous, consequently it does not form the extensive areas of grass that that species does, but occurs more sporadically. It is found only in the Malay Peninsula, Java, Sumatra, Borneo, Celebes, Papua, Philippines, Vavau, and the New Hebrides.

As it does not grow in mass, it is not gathered by man for package or litter, nor has it the advantage of fire which is possessed by *I. cylindrica*, for

fire, as I have said, not only does not injure that plant at all, merely causing it to produce flower and fruit, but also it eliminates other competitors. Hence the abundance of *I. cylindrica* in comparison with *I. exaltata*, which has to depend exclusively on its spread by wind.

Miscanthus is a reed-like grass with a tall loose panicle of small spikelets surrounded with long silky hairs. The whole inflorescence is about 6 or 7 feet tall. It inhabits river banks usually, but 1 species is, in the Malay Peninsula and Borneo, a dweller in open woods. In *M. japonicus* the hairs are rather shorter than the spikelet. However, as the tall spreading panicle waves in the wind, the spikelets are readily diffused. It is found in the Malay Peninsula and all the larger Malay Islands, New Caledonia, Tahiti, Solomon Isles, Samoa, Cook Isles. *M. sinensis* also occurs on many of the Malay Isles, but in Fiji and perhaps some other of the Polynesian isles it has apparently been introduced, and these species are replaced by the closely allied *M. nepalensis* in India.

Saccharum Narenga and their allies have large panicles of abundant, very small spikelets, with long silky hairs rising from the base and much longer than the spikelet, and these are usually very widely diffused, while *Sclerostachyum*, with hairs shorter than the rather hard-glumed larger spikelet, are much more local plants, as their flight powers are more limited. There are 2 species, one Indian, and the other, *S. Ridleyi*, is only known from a single spot on the banks of the Pahang River, where it occurs in large clumps; but though abundant there, it has never been met with anywhere else. We may contrast it with the great Elephant Grass, *Saccharum arundinaceum*, with its silky plumed spikelets, which is not only very common along this river, but also occurs in China, India and the Malay region to Papua.

Saccharum spontaneum, in which the spikelets are very small, with long silky hairs, is widely spread from Algiers through Egypt to Africa, and to India, China, Formosa, Tonkin and Java, Halmaheira, Celebes and the Philippines. It reached Krakatau from Java in 1897. Its absence from the Malay Peninsula is probably due to the want of the open country in which it habitually grows.

Gynerium and *Cortaderia*, the Pampas Grasses, have the spikelets very small and light, and covered with long silky white hairs in the female flowers only. The male flowers are not plumed, so that the flight of the pollen is not interfered with. They are natives of the open country in South America.

Triraphis madagascariensis is a beautiful tall silky plumed reed, growing by streams or in open woods in China, India, the Malay Peninsula and islands, to the Philippines and tropical Africa and Madagascar, Mauritius and Comoro Islands. It is the only species which is widely spread, the rest, which have spikes or panicles much shorter and more condensed, being Australian or African, and there can be no doubt that the evolution of its fine, tall silky loose panicle is responsible for its wide dispersal.

Calamagrostis.—In this genus the spikelets are often not plumed at all, or have hairy glumes or basal hairs too short to be of much use in flight, but *C. epigeios* has a whorl of hairs long and silky at the base of the spikelet, twice as long as the glumes. This reed-like plant has a rather dense panicle, and grows in open woods. It is a native of Europe, Africa and India, and seems to be the species best furnished for flight, as well as the most widely distributed.

Ischaemum nativitatis.—This is a short grass about 1 foot tall, with terminal spikes of hairy spikelets with long awns. The spikes break up into joints and are blown about by the wind along the coast, and accumulate in little holes or depressions in the coral rocks. It is peculiar to Christmas Island, and is not allied to any species in the Malay or Australian regions. Its only allies are natives of the seashores of the Polynesian Islands. As grasses, furnished with much better apparatus for flight, seem to be quite unable to cross a hundred

miles of water, it is impossible to attribute its occurrence in this distant island to wind, though its dispersal *in* the island is certainly due to this element. It possibly came by sea, though this is hardly probable, or possibly by adhering to a sea-bird. It is, however, very difficult to account for its presence. The remainder of the genus have the spikelets blown along the ground, and some appear to be carried about in fodder. One, *I. muticum*, is certainly sea-dispersed, but it is specially adapted for this purpose, and the spikelets are glabrous, polished and smooth.

Tricholaena is a genus of African grasses of which one species, *T. Teneriffae*, occurs in the Canary Islands, as well as from North Africa to Arabia. The spikelets are small and plumed from the base, the hairs in *T. rosea* being about ¼ inch long, the spikelet being half the length. The plumed spikelets, therefore, are quite light and easily blown away. *T. rosea* was introduced as a fodder grass into Selangor at the gardens of Batu Tiga, and many years later I found the plant thoroughly established on the rocks of the Batu caves, where quarrying was taking place. I have little doubt that the fruit had been brought there accidentally, either by the railway or attached to clothes, etc. It has now spread about over the rocks undoubtedly by the wind.

Pennisetum macrostachyum (*P. elegans* and *Gymnothrix elegans*) is a large bushy grass with a long spike of spikelets on a tall slender peduncle. The spikelets, ¼ inch long, are surrounded by bristle-like hairs 1⅕ inch in length. These hairs are silky in some forms, but rather stiff in others. Detached spikelets blown into the air fly in a manner resembling the plumed fruits of *Compositae*. The grass grows in Sumatra, Borneo, Celebes, Papua, the Philippines and Solomon and New Britain Islands. This was one of the first grasses to reach Krakatau after the eruption, and as it seems mainly an island plant, it has probably reached the above-mentioned islands by wind.

Pogonatherum saccharoideum.—This pretty little tufted grass, known in the East as the Bamboo Grass, grows on damp or dripping rocks and streamlets all over the East Indies, and is especially common on roadsides where the streams come down from the mountains. It is usually about 6 or 8 inches tall, and bears slender spikes on wiry peduncles. The spikelets are silky at the base, but the silky hairs are not long enough to aid materially in the flight of the spikelet, in which the organs utilised for flight seem to be mainly the long hair-like awns borne by Glumes II and IV. As the whole spike breaks up and two or more spikelets often become entangled together by the awns, the light mass is easily blown away along the roadside banks till it reaches a suitable damp spot. It is found in India, China, Formosa, and the whole Malay region to Australia and was one of the first grasses to reach Krakatau.

Perotis latifolia is a seashore grass which I think owes its dispersal to its very slender awns. The spikelets are arranged in a long spike, and are very small and light, and blow away easily. Each possesses 2 hair-like awns from ⅛ to ½ inch long. It ranges from Baluchistan, through India and China, the Malay Peninsula and islands, to Australia, and is also African. It occurs on sandy sea coasts, and probably originated in Africa, from whence it has spread in an easterly direction.

Glumes Hairy.—Very many grasses have the outer glumes covered with hair, but in a comparatively small number is the hair sufficiently long and silky to be of any use in transporting the grain. One of these is the desert grass *Lasiacis hirsutus*, in which the outer glumes are covered with long white silky hairs, so that the whole spikelet can be blown along the sands. It is found in Cyrene, Egypt, Afghanistan, Africa to Suakin, and the Punjab, and has been met with in Perim Island.

Another grass with plumed hairs on the spikelets is *Digitaria barbata*, a sand-hill grass with long slender spikes of distant, rather flat lanceolate

spikelets, fringed with long white hairs on the two outer glumes. It is found in sandy places in China, Formosa, the Malay Peninsula, Java and Siam, but does not seem to be very common. The spikelets are easily detached and can be readily blown along the sands.

Grasses with Plumed Awns.—These are confined to the genus *Stipa*, and to only a few species of that genus. *S. pinnata* has an awn 9 inches long, of which 6 inches are beautifully feathered, so that it can be blown to some distance; but it also serves as a lever to turn the spikelet and cause it to bore into the ground when it has come to rest, the wind acting on the horizontal plume. The plant occurs in open localities, moors, or rocky places all over Europe from Sweden south to the Mediterranean (absent from Britain), and North Asia to China and North India (Pl. XI, fig. 5).

S. pulcherrima, of Eastern Europe, has a similar plumed awn 8 inches long, 6 inches of which are plumed.

Plumed Styles.

A certain number of plants, mostly inhabitants of plains or open mountain slopes, are dispersed by the elongate plumed styles which function as flying organs. Among these, certain species of the genus *Geum* are the most interesting. These are herbs of the order *Rosaceae*, abundant and widely spread over the north temperate zone in Europe, North Asia and Africa, and North America, radiating down the mountain chains of the Himalayas and the Andine range to Fuegia.

In the method of dissemination the plants fall into two groups. In one group the numerous crowded carpels are each provided with a single slender glabrous style which in fruit is hooked at the tip, and is by this means readily attached to passing animals. In one species the style is provided with retrorse bristles, which also serve to attach it to the fur of a passing animal. These are described under the account of Adhesive Fruits (p. 577). In the second group the style is very long and slender, and the whole carpel is thickly hairy. The style, about 2 inches long, is fringed with long silky hairs, and exactly resembles that of *Pulsatilla* and *Clematis*. The terminal hook of the style in the first group is wanting, and the style is longer and more slender.

In many of the species with hooked glabrous styles the carpels are hairy, the hairs pointing forward. Kerner attributes the occurrence of hairs round the carpels, or at least in the interior of a flower, to a necessity for protecting the secreted honey from the attacks of undesirable insects which take the honey without pollinating the stigmas of the flower, but he also points out that the dry coat of hair protects succulent tissues exposed to the sun's rays, from overheating and excessive exhalation of moisture. Dealing with foliage, he points out that the plants of the alpine districts and the deserts suffer most from the drying up of the soil by the sun, and that here a great development of a covering of hairs occurs on the leaves. Now, in *Geum* the flowers open widely to the sun, and it seems likely that the object of the hairs on the pistils is to prevent radiation and excessive exhalation of water from the soft tissues of the ovaries. The carpels are very closely set in the flower, and fully exposed to the sun, so that the close mass of hairs practically covers the whole head of carpels with a continuous coat.

Another important use of hairs to the plant is as a protection from drops of water lying in actual contact with the outer tissues and causing injury by decay, or by the action of the sun's rays on the drop acting as a burning-glass.

I am inclined to think that both the last two uses are the objects of the hairiness of the pistils, more especially as it is in the alpine and arctic forms and

in those of dry desert regions that we find the greatest development of hairiness both in *Geum* and *Pulsatilla*.

I take a series to show the plan of evolution from the glabrous hooked style to the beautifully plumed style in *Geum*.

G. urbanum.—In this the ovary is thinly hairy, the style $\frac{1}{4}$ inch long and hooked, quite glabrous. Lowlands, meadows, roadsides. *G. rivale*.—Here the base of the style, as well as ovary, is hairy; the tip of the style above the curled portion which forms the hook when the fruit is ripe is also hairy, but this is speedily broken off (Pl. X, fig. 2). *G. rotundifolia* and *G. Peckii* have the ovary very hairy, style hairy half-way, tips glabrous, hardly hooked. They are natives of Sitka and Arctic America. *G. pallidum*.—Style is hairy to the tip, which, however, is hooked in fruit. North America. *G. reptans*.—Style plumed, slightly hooked. Japan and North America. *G. aremonoides*.—Japan and Arctic America, *G. pentapetala*, of Japan, *G. montanum*, *G. alpinum*, and *Bulgaricum*, of the mountains of Europe (Pl. X, fig. 1), and *G. triflorum*, of the mountains, prairies and limestone rocks of North America, have beautifully feathered plumed styles with no hooks, and the fruits in these are wind-dispersed.

It will be noticed that in the alpine and arctic regions, where large mammals are scarce or absent, the styles are not provided with a hook for dispersal by attachment to fur, but they are plumed for wind-dispersal.

Thus in *Geum* we have a series of herbs in which the carpels, slightly separated, are covered with hairs to protect them in the flower from injury by water collecting on or betwen them, and for prevention of too great exhalation of water from their tissues.

In the lowland open country districts, where mammals are common and

and Siam, the Philippines and Australia, down the African mountains to the Cape and from North America to Chile. The section or genus *Pulsatilla* is found in Europe, the Himalayas, South Africa and North America.

Like *Geum*, though of a totally distinct order (*Ranunculaceae*), the female organs consist of a number of separate carpels, each containing a single ovule, forming, when ripe, small achenes. The styles are short and in some instances hooked (*A. crassifolia*, of Australia), and, like the achenes of *Ranunculus acris*, which they much resemble, are dispersed by adhesion to animals' fur.

Another group of *Anemone* (*A. narcissiflora*, *A. polyanthes*, *A. tetrasepala* and *A. elongata*), natives of Europe and temperate Asia, have umbelled flowers on long stalks, the achenes being flattened, rounded, with a thick edge, quite suggestive of the form of the fruits of some *Umbelliferae*, such as *Heracleum*, and these are doubtless spread in the same way as those of the Hogweed, by gusts of wind.

In the third series the achenes, when ripe, are covered with short woolly hairs, by which they are wind-dispersed, as is described on p. 144. They are found in Europe, temperate Asia, India and North America.

Finally we have the section or genus *Pulsatilla*, in which the style is plumed elegantly, and by this modification the achenes are dispersed.

It will be noticed that the greater part of the genus *Anemone*, in the large sense, owes its wide distribution to the action of wind, though to a minor extent to adhesion to the fur of animals. The plants grow in open country, mountain-sides, or open woods, and are mostly fairly tall herbs whose fruit would be readily exposed to air currents.

In all but *Pulsatilla* the style is very short, and where the ovaries are closely set together, so that no water can penetrate between them, the carpels are usually glabrous. In *Pulsatilla*, however, the styles are long, slender and hairy all over, and when the achene is ripe the style has developed a hairy plume about 2 inches in length, and closely resembling that of the plume-styled *Geums*. These plants are mostly inhabitants of cold northern countries, where they grow on rocky, stony or dry slopes or chalk downs. *P. vulgaris* grows on chalk downs in England and other parts of Europe, and there are 4 or 5 other species in Europe, *P. albana* in the Himalayas, *P. capensis*, *P. caffra*, *P. Fannini*, in South Africa, and 2 species in North America.

I have not seen any intermediate forms between *Pulsatilla* and the other *Anemones*. In Africa we find a number of species of the genus *Clematopsis*, erect branched shrubs with large purple flowers, somewhat like those of *Pulsatilla*, and with long plumed styles as in those plants. This genus leads towards *Clematis*, some of which have similar flowers, and all have the same kind of achenes with long gracefully plumed styles. Some are erect bushes, but far the larger number and the most widely spread are climbers. The genus with the allied *Naravelia* of tropical Asia is found practically all over the world, including the Polynesian Islands, Fiji and New Caledonia, Timor, Celebes, etc., but is absent from remote islands. In tropical Asia they are mostly found rather sporadically on mountains, and the species range widely, *C. Pickeringii* from Celebes to New Zealand, and Fiji. The plants seem to be absent from oceanic islands, and it is difficult to see how a species like this has reached these islands (Pl. X, fig. 7).

One can have little doubt that the *Clematis* has evolved from *Clematopsis* of Africa, and that that in turn has been derived from *Pulsatilla*. Its wider distribution is due to its having taken on a climbing form, so that the great panicles of fruits are fully exposed to the winds, and the achenes with their silky plumes are more widely and readily dispersed.

A somewhat similar feathery plume is evolved in some species of *Geraniaceae*. In the genus *Monsonia* the species inhabiting South Africa have the fruit in all

respects like that of *Erodium* and *Geranium*, a long beak composed of lengthened carpellary points and the prolonged style. The carpels dehisce longitudinally and eject the seed violently, as is described when dealing with Explosive Fruits (p. 663). But in some species of *Monsonia* inhabiting deserts, *M. umbellata* of tropical Africa, *M. nivea* of the deserts of Algeria, Egypt, Arabia and Siam, and *M. heliotropioides* of Arabia and Baluchistan, the inner face of each carpellary beak is plumed with long silky hairs, by which the seed is transported by wind over the flat plains.

Fruits Dispersed by Carpellary Hairs.—It is not rare to find fruits in which the carpels are hairy, the object of which is already explained, when dealing with the account of the carpels of *Geum*, under Plume-Styled Plants (p. 141). Though this hairy covering occasionally persists till the fruit is ripe, more usually it disappears altogether. In some cases, however, it not only remains on the carpel, but increases in length and becomes woolly—that is, the hairs become soft and curly and act as a flying organ. For this purpose it is necessary that the carpel remains quite small and is 1-seeded. The distance of flight of such fruits is not very great, as the hairs are not long in proportion to the size of the fruit, but the flight is far enough to be of great use in dispersal.

In the *Anemones* we have an excellent example of this. A certain set of these have the numerous close-set achenes covered with soft, woolly white hairs when ripe, borne on a more or less conical or cylindric receptacle. In *A. cylindrica*, of North America, this receptacle is as much as 1½ inch tall when the fruit is ripe, and as the coloured sepals have by this time fallen, the little fruits are fully exposed to the wind, and can be blown to some distance. In nearly all these woolly-fruited *Anemones* the stem is tall and rather stout, so that the cone of fruits is held up well above surrounding foliage. They are inhabitants usually of open pastures and mountain-sides. The achenes when ripe are blown away gradually, a few at a time, the lowest ones on the cone going first. I have only seen them in gardens blown to a few feet distant, but I have no doubt that in a wild state they will travel much further (Pl. X, fig. 9).

A few species like *A. coronaria* and *A. baldensis* and *A. hortensis* are found in Europe. *A. sylvestris*, *A. japonica* and *A. vitifolia* inhabit temperate Asia, Siberia, China and Japan, the last-named ranging from India to China and the Philippines. There is 1 species, *A. Thompsonii*, in Kilimanjaro, Africa, and 7 species of this group of *Anemones* in North America.

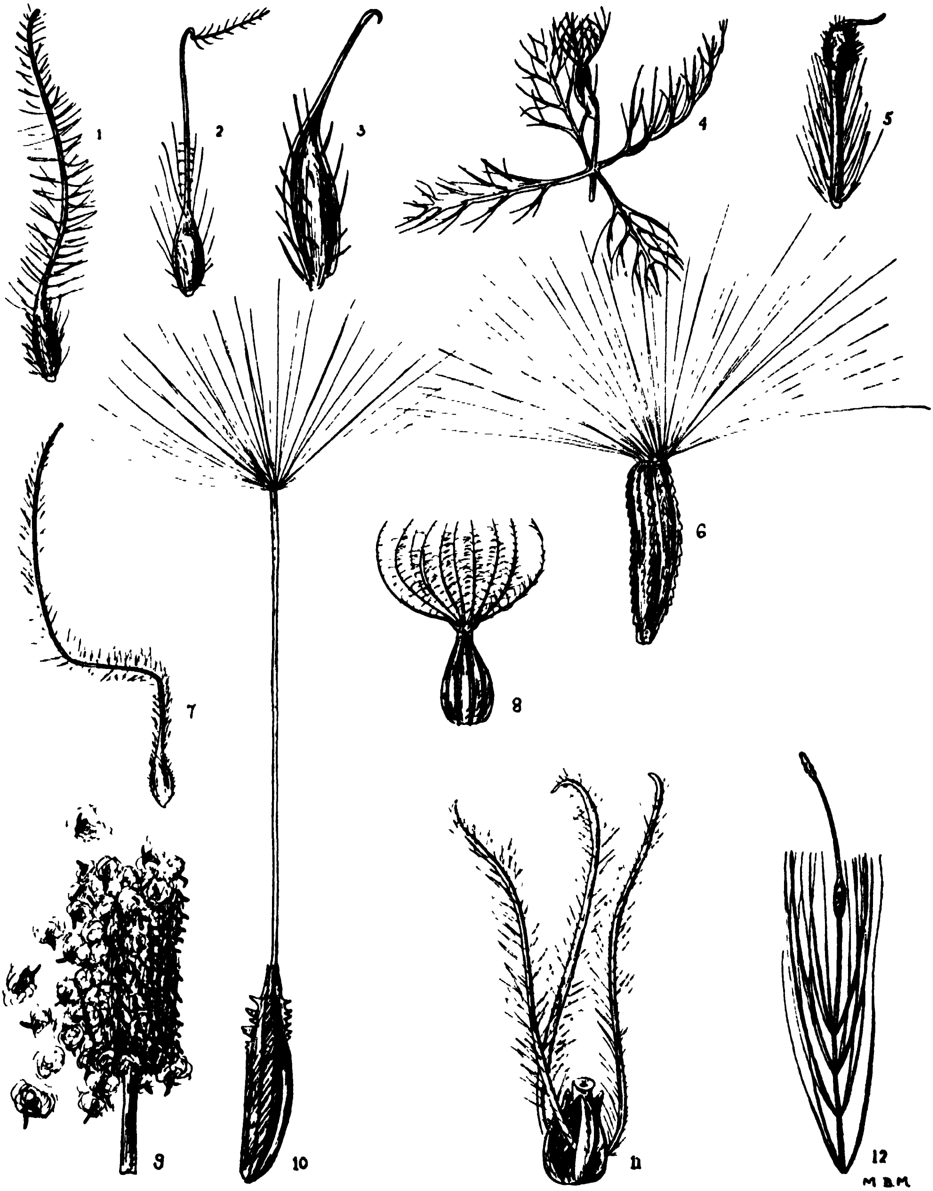
Sepaline Plumes.

The order most lavishly furnished with sepaline plumes is that of the *Compositae*, of which a very large number are widely spread by the pappus, a modification of the sepals; but before dealing with these I will mention a few plants of other orders which have plumose sepals by which they are dispersed.

Though many of the *Umbelliferae* have fruits dispersed by wind, they have, as a rule, little but their lightness, and sometimes a dilation of the lateral ribs of the fruit, to aid them in their dissemination. There is, however, one curious little plant which has the addition of plumose sepals. It is a small annual herb of the Mediterranean region and Palestine—*Lagoecia cuminoides*. In this plant the fruits form a soft round head about ½ inch through. At the base of each fruit are 4 pectinate light bracts surrounding it, and above the fruit are 4 similarly feathered sepals. The fruit breaks off below the bracts, and with the aid of these, and the plumose sepals, it can be readily blown away by the wind (Pl. X, fig. 4).

Valeriana and *Centranthus* (*Valerianaceae*) are herbs in which the fruits are plumed by the modification of the sepals, or rather the free portion of them.

PLATE X.



WIND-DISPERSAL. PLUMED FRUITS.

FIG. 1.—*Geum Bulgaricum.*
,, 2.—*G. rivale.*
,, 3.—*G. urbanum.*
,, 4.—*Lagoecia cuminoides.*
,, 5.—*Platanus acerifolia.*
,, 6.—*Sonchus oleraceus.*
,, 7.—*Clematis vitalba.*
,, 8.—*Valeriana officinalis.*
,, 9.—*Anemone vitifolia.*
,, 10.—*Taraxacum Dens-Leonis.*
,, 11.—*Myzodendron brachystachyum* (after Hooker).
,, 12.—*Typha latifolia.*

[*To face p.* 144.

They are herbs of various heights, from quite dwarf plants to those which are 3 or 4 feet tall, with terminal panicles or corymbs of small flowers. The fruit bears at the top from 5 to 15 rather slender bristle-like processes plumed with hairs which, till the fruit is ripe, are curled in over the top of the fruit and then expanded, so that they readily float away on the wind. The plants are found in open woods, mountain slopes and river banks in the north temperate region (Pl. X, fig. 8, *Valeriana officinalis*).

Centranthus ruber, the common red Valerian, is usually a rock or dry bank plant. The fruits are readily dispersed by wind to some distance. I have found plants growing on the cliffs at Swanage at a distance of 100 yards from their nearest species.

C. calcitrapa, with similar plumes, occurs in Madeira and the Canaries, as well as Europe, but it is a plant whose fruit is much dispersed in cereals, and it has occasionally appeared in this way as an alien in Britain.

It is, however, in the great order of *Compositae* that the most important and striking evolution of the plumed fruit is exhibited. Most of the species are herbs, sometimes shrubby at the base, or completely shrubby, and not rarely scandent, or, strictly speaking, sarmentose, but some are trees of no great size, the biggest being the tree Vernonia, which grows about 60 feet tall.

The plume-fruited *Compositae* are found all over the world, from the Arctic regions to the south, but are absent from the thick rain-forests. They are really characteristic of open country, steppes and plains, where they attain their fullest developments. In the equatorial forest region they become scarce, and only occur on cleared ground and on the borders of the forest. The flowers are borne in compact heads, usually containing a good number sessile on a receptacle which is surrounded with an involucre of bracts which are generally reflected or expanded when the fruit is ripe, so as to afford full play to the wind. The fruit is a 1-seeded achene, inferior (i.e. enclosed in a tubular adherent calyx), with free sepal points, which in some species form adhesive organs, but which in the plume-fruited ones develop into a number of very fine hairs (the pappus), in many cases (*Tragopogon*, *Chevreulia*, etc.) spreading from the top of a long hair-like process from the apex of the achene. These slender spreading hairs are often armed with minute processes, and are sometimes viscid when wetted (*Senecio vulgaris*), and by this means, as also frequently by recurved hooks or forward-pointing hairs on the body of the achene, the fruits, falling on damp soil, are anchored to the ground in a place suitable for germination. If the achene comes to rest on dry hard spots, or on leaves, it lies on its side, partly raised by the projecting hairs, and can be blown further along the ground by following air-currents, or, if light, can actually be raised again in the air and continue its aerial wanderings. In rain or very wet air the plumes collapse and the achene falls.

The possible distance of flight (as is shown in the account of the island species) being very great, is responsible for the wide distribution of these plants. At the same time it must be pointed out that many *Composites* which have an extraordinarily wide dispersal are not plumed. These, however, owe their dispersal to human agency by the adhesion of their hooked, glandular or spiny sepals to clothes, the fur of domestic or wild animals, or birds' feathers.

The order contains some of the largest and most widely distributed genera we have, such as *Senecio*, with about 900 species distributed all over the world, except in the coldest and hottest places; *Vernonia*, about 400 species, all through the tropics of both worlds; *Erigeron*, over 100, chiefly in the temperate regions, but also in the tropics; *Aster*, about 400, chiefly north temperate regions and mountains in the tropics, with a number of closely allied genera in the southern hemisphere; *Crepis*, 140, chiefly in the north temperate region, but spreading southwards into cool places in the tropics.

Several species, partly aided by man, partly by wind, have now spread into most parts of the habitable globe. Such are *Taraxacum dens-leonis*, *Sonchus oleraceus* and *S. asper*, *Erigeron linifolius*, *Crepis virens*, *Tridax procumbens*. Of some of these I give a fuller account, as they are of some interest.

Taraxacum dens-leonis (Dandelion) (Pl. X, fig. 10).—This plant has an extremely wide distribution in most temperate climates, and in some parts of the world has invaded the tropics, but it owes a good deal of its wide dispersal to human agency, having been used as a medicinal or salad plant for a very long time.

It occurs in a wild state over the whole of Europe and north temperate Asia, and Arctic America, and again apparently wild in the extreme south of South America, from Chile to the Magellan Straits, and in New Zealand. Except as an escape from cultivation, it is absent from all of South America, except the extreme south, West Indies, Africa, Peninsular India, the Malay region and Australia. It appears in the Interglacial period in England, and consequently may be considered definitely as of north temperate origin. It is very variable in size and form of leaf, and a large number of species have been made of it, but I do not think that there is more than one genuine species. The most distinct varieties are the mountain and antarctic forms, with narrow, often nearly or quite entire, leaves, but these seem to pass into those with cut and dentate leaves. There are many forms of this class in the Himalayas and Thibet. The lowland and cultivated forms have large dentate leaves. The plant, however, varies very rapidly in these points. The cultivated form from Europe was introduced into the vegetable garden on Penang Hill between 1889 and 1892, at an altitude of 2,000 feet. From here it spread a short way and established itself on banks. In spite of its plumed fruit, it has not spread ½ a mile away from its original planting in 35 years, but it very quickly altered in form to a small closely-cut leaved variety, resembling the form known as *T. laevigatum*. Specimens collected about 1925 were identified at Kew as *T. indicum*. It does not now at all resemble the large-leaved original plant. Another form, evidently escaped from cultivation, which I collected on a roadside in Java, has been identified as *T. mongolicum*. The plant appears to be very plastic.

It has been suggested, chiefly from the occurrence of the peculiar antarctic form in the Magellan Straits and New Zealand, that *Taraxacum* was evolved in the Antarctic regions and migrated northwards to the north temperate zone. Its absence from Australia, the Philippines, etc. (except as a late introduction), and its presence in England in the Interglacial period, seem to militate against this, and I would rather suggest that its origin lay in north temperate Asia, and that it descended to the Antarctic regions from Arctic America by way of the Andes, though as yet it has not been found anywhere between.

The Dandelion, when flowering, erects its peduncle so as to show off its brilliant golden flower-head to pollinating insects. After fertilisation it lowers it again till it rests on the ground, re-erecting it when the fruit is ripe, so as to expose the fruits to the wind. The flight of the achenes, in an ordinary light wind, is only for a comparatively short distance, usually about from 12 to 15 yards. They are stopped at once by collision with bushes and hedges, and fall to the ground, the achene being detached from its parachute. The achene is provided with short processes in its upper part by which it may adhere to clothing, etc., or may be anchored in the crevice of a wall, but it is more readily detained by the plume, the hairs of which are provided with short processes.

I have noted that in long grass the drifting fruits attach themselves lightly to grass blades with which they come in contact, but are retained so delicately that a slight puff of wind is sufficient to carry them further.

Peacock (in "Fox Covert Studies") includes it among plants he has found in mud attached to boots, and so carried about.

The fact that the pappus is borne on a long stalk (as is also the case in *Tragopogon*) causes it to be more fully exposed to the blasts of the wind, and it then has an advantage over the shorter-plumed stalkless fruits of *Hypochaeris*, etc., not only because it stands erect on its receptacle, but also because when it falls on the ground, resting as it does on the tips of the hairs on one side, it is readily blown further along the ground.

Sonchus.—The Sow-thistles differ from *Taraxacum* in being much taller, 2 feet or more in height, and in possessing small fruits with a short abundant silky plume not supported on a stalk. There is little doubt that these small plumed fruits actually fly farther than such fruits as those of *Taraxacum* and *Tragopogon* with an umbrella-like stalked plume, and in doing so rise in the air. It is clear that the three species, which are as common as weeds of cultivation, when introduced into a country are diffused with great rapidity over open ground, but I have no evidence that their plumed fruits are carried to any very great distance.

The genus is most strongly represented in Africa, and of the 11 species of Europe, *Sonchus oleraceus*, *S. asper* and *S. arvensis*, weeds of cultivation only, and one tidal river-bank species, *S. palustris*, are the only species widely diffused over Europe, the remainder being practically confined to the Mediterranean area. The only species known fossil in Europe is *S. arvensis*, which occurs with weeds of cultivation in Neolithic times. (Pl. X, fig. 6, *S. oleraceus*.)

An interesting point about the Sow-thistles (*Sonchus*) is the extremely wide spread of *S. oleraceus* all over the cooler parts of the world, including a number of the oceanic islands, though in most of these localities we have no very early records of its presence. I give some of these, with the earliest dates of its appearance I have been able to get:—Fiji Islands (1845), New Caledonia (1861), Tongatabu (1874), Easter Island (1911), Meyer Island, Kermadec (1885), New Zealand (1847), Australia (1817), Tristan d'Acunha (1816), Aldabra, Picard Isle (1916), Cape Verde, Canaries, Madeira, Juan Fernandez. In most, if not all, of these islands there is reason to believe that it owed its introduction primarily to man, but, once introduced, it has spread by its own plumes. In New Zealand and Australia it seems to have been introduced after the first settlers came. Cunningham found it in Australia in 1817. He writes in his diary, of Mount Lachlan: "*Lotus major* with *Sonchus oleraceus* are very abundant, also *Linum usitatissimum*." Now, cattle had run wild in this area before 1801, and might have accidentally brought it to this spot. The occurrence of the Flax (*Linum*) with it, suggests a patch of cultivation, for the Flax is not known in a wild state at all, and is probably an evolution of early cultivation. Moseley (in "Notes of a Naturalist on the Challenger") records that Easter Island was a sheep station in 1896. In Tristan d'Acunha, Carmichael found it abundant in 1817, but Thouars, who collected there in 1793, does not record it, though he mentions the lettuce and radish as occurring there. Vegetables were planted there, as in many islands, by the voyagers in the early days, and there were cattle and sheep there also. On Inaccessible Island, where Moseley found it, two Germans had settled and probably introduced it. There had formerly been pigs, goats and dogs there. In Juan Fernandez goats were introduced very early, and cattle by 1879. Mr. W. R. B. Oliver, in giving a list of the very limited flora of White Island, near New Zealand (*Journ. Linn. Soc.*, xliii, 46), records this plant as occurring in detached masses near the gannet colonies. The flora is very scanty owing to the great abundance of hydrochloric fumes, the island being entirely volcanic. Here it seems that it must have been introduced by the plumed seed adhering to the gannets.

In Aldabra Islands (Mascarene group), Picard Island, where it occurs, there

was a settlement by a European who kept goats there and grew vegetables, including tomatoes raised from English seed.

In almost all of these island localities sheep or goats have been introduced before the plant has been recorded for the island, and I should suggest that it owes its presence there in most cases to the attachment of its fruits to the wool or hair of these animals, or possibly to its being brought in the fodder for them. The fruits might in some cases have been brought attached to the clothes of man, or to sacks, etc., or in vegetable seed brought from Europe or elsewhere.

Sonchus asper, the next most widely distributed species, is absent from most of these islands, but a very striking form occurs in Australia and New Zealand. It is very large and coarse, and is a perennial plant (unlike the typical annual form), and is stoloniferous. It occurs chiefly—or perhaps always—on the sea-shores. In Chatham Island there is a still more robust form with much larger leaves, called *Sonchus grandifolius*. This appears to have been used as a food plant by the Maoris, who have a native name for it. This plant differs from typical *S. asper* in its much greater size, and its perennial and stoloniferous habit as mentioned above, and in the outer florets being pale purple, and the presence of short-hooked processes on the outer involucral bracts, but I have seen a specimen from Abyssinia with somewhat similar processes. *S. asper* is widely distributed over Europe, Africa and Asia, but chiefly on the mainlands. It does not occur in Polynesia or southern South America except as an introduction. It is recorded among aboriginal weeds of Tonga and New Zealand by Cook's botanists, 1768 to 1780. It is difficult to see how this plant first reached Australia and New Zealand so early. There is no plant allied to it nor any species of the genus in that part of the world, except the obviously introduced *S. oleraceus*. I can only suggest that it was originally introduced from Europe in very early days and has become remarkably modified since.

Sonchus arvensis is much less widely distributed than either of the other two, and apparently has as yet only reached North America and a few other spots by accidental human agency.

In the latter two species the fruit, except for 2 ribs on each side, is quite smooth. In *S. oleraceus* the 2 edges of the flattened achene and the 3 central ribs on each side are papillose, and between these ribs are 5 raised transverse lines, and it is by these small papillae, which bear deflexed hooks, that the fruit adheres to the wool of sheep, hair of goats, and clothes of man, and it is to this minute modification that *Sonchus oleraceus* owes its very wide distribution rather than to its plumed pappus, though there is little doubt that it has also been introduced in many places like Tosari, in Java, in vegetable seeds.

Vernonia cinerea is a low, slender annual herb with a loose panicle of small heads of violet flowers. It is very common as a weed all over the warm parts of the tropics, generally found in cultivated ground and roadsides. It occurs all over tropical Asia and Africa as far north as Arabia, and in the West Indies and South America, tropical Australia and Polynesia. Of islands, it occurs in Cape Verde, Socotra, Chagos, Laccadives, Maldives, Minikoi, Krakatau, Cocos-Keeling (1912), and many Polynesian islands. It was absent from Christmas Island and Fernando de Noronha. It undoubtedly reached Krakatau and probably some of the other islands by wind, but it certainly owes its large distribution to the agency of man, especially in such places as Cocos-Keeling Isle, where it has only recently appeared.

In many of the *Amarantaceae* the perianth lobes, and often the bracts also, are provided with hairs which increase in length in fruit and form dispersal organs. Frequently when the fruit (a utricle containing a single seed) is ripe, the whole flower is covered with the long silky hairs, which are sometimes (*Aerua*) curly and wool-like. In most of these plants the crowded little flowers in racemes or panicles are detached and blown away over the seashores or

deserts in which most of them grow. Many are herbaceous and prostrate or creeping, a few shrubby, and some are scandent on bushes or trees. The stiff perianth lobes have hairs at the base inside or outside, or the hairs are apparently borne on the short pedicel of the flowers. In *Saltia*, a plant of Aden, the plumes appear to be bracts and pedicel with 3 or 4 abortive flowers, and this plume only occurs in the female flower. *S. sericostachys*, an African climber, has a long pendent panicle in which, in the flowers, are elongate bristles, silkily plumed like feathers. In *Calicorema* the hairs are about ½ inch long. This is a shrubby bush 1½ feet tall.

Aerua is a genus of several widely dispersed herbs more or less prostrate, or more rarely scrambling over bushes. They inhabit dry open spots in Africa and India. The flowers are about 2 mm. long and borne in dense white spikes. The sepals are papery, ovate or lanceolate, covered at the base with a pure white cottony wool of curled hairs. When the fruit is ripe the flowers are detached and resemble small pellets of wool, very light, and are readily blown away. I have also found the flowers, containing ripe seed, deeply buried in sheep's wool, and there is little doubt that they are widely dispersed by these and other animals, which probably accounts for their extensive distribution and abundance.

Ae. scandens and forms of it occur all over India and Burma, Siam, Cambodia, Philippines, Timor and Timor Laut.

Ae. javanica, in which the small flowers are very woolly, occurs all over Africa from Algeria, Arabia, Socotra and Cape Verde to South Africa and Madagascar, Syria, Baluchistan to India and Burma, very abundant on sand-banks and in deserts.

Indeed, the whole series of these hairy-fruited Amaranths is characteristic of sand-banks and deserts, where the little dry flowers with their solitary seeds can be drifted about by the winds.

Many, *Chionothrix*, *Saltia*, *Sericocoma*, *Calicorema*, are African; *Aerua*, Africa and Asia; *Ptilotus*, Australia; *Gossypianthus*, a prostrate herb, Mexico; and *Iresine*, a climbing plant, South America and the West Indies.

Leucadendron argenteum (*Proteaceae*).—This silver-leafed shrub or tree has an inflorescence consisting of a cone of bracts, with tubular flowers having 4 feather-like sepals. The ovary is 1-seeded, and is enclosed in the rounded calyx tube. The 4 sepals are persistent in fruit, and then about ½ inch long, simple plumes of a slender stalk fringed with long brown hairs. The nut when ripe is flattened, ovate, nearly ½ inch across, with the slender, slightly hooked style adherent to it. The globose calyx splits from the base upwards, and the fruit falls, but is prevented from becoming detached from the calyx by the bent stigma, so that it hangs below the plumed calyx, and is drifted away by the wind. This system of dispersal is described by A. Nestler in "Der Flugapparat von *Leucadendron argenteum*" (*Bot. Jahrb.*, 1892-3, p. 325).

The fruits seem to me to be rather large and heavy to be borne to any distance by the plumes, but Marloth confirms Nestler's statements, and says that the tree grows in very windy, open spots at the Cape of Good Hope, and the fruits fall from the bracts of the inflorescence and are borne away by the wind. The same principle is adopted by the allied genus *Mimetes*, but in this the calyx tube is cylindric and the whole fruit smaller. In some of the other *Proteaceae* the ovary itself is plumed with long hairs which act as flight organs.

Fruits with Hairs at Base.—*Typha* (*Typhaceae*).—The Reed-maces are very widely distributed over the world, which is not surprising when we consider the vast number of extremely light plumed fruits which a single plant will produce. The inflorescence consists of a dense spike of very small female flowers and a shorter similar terminal spike of males. The fruits are

minute achenes on a slender gynophore covered with long hairs, short in flower and becoming long in fruit (Pl. X, fig. 12). These hairs were formerly believed to represent a perianth, but, owing to their number and irregularity, they are not so considered now. Being extremely small and light, the fruits can be borne by the wind to very great distances, and the genus is very widely distributed. About 10 species are recorded, all closely allied, the most widely diffused of which is *T. angustifolia*, of which there are several local forms. It is found in Europe, North Africa, Palestine, the Canaries, Madeira, tropical and South Africa, Seychelles, North Asia, India, Ceylon, Java, Papua, Philippines, Australia, Fiji, Kermadec and Norfolk Islands, New Zealand, North and South America, and the West Indies.

These plants are usually missing from oceanic islands, but there is generally no suitable habitat for them there. Besides being distributed by wind, the seeds are said to be disseminated by attachment to the plumage of water-fowl, and the rhizome is also dispersed by fragments becoming detached and floating away. The fruits are probably the lightest of any plume fruits; but though, besides being produced in vast numbers, they have, as it would appear, every advantage for wide and abundant dissemination, the plants are not nearly so widely dispersed or as abundant as the common Reed (*Phragmites*). The reason for this is, I assume, the greater adaptability of the Reed, which can grow and thrive successfully in all climates from the arctic region to the equator, and succeeds equally well along river banks, swamps, pools and seashores. *Typha* is practically confined to stagnant pools or slow-moving water, and its rhizome requires complete and permanent immersion. Nor does it thrive in very hot climates. In fact, it is much less adaptable to circumstances than the Reed. In England, at least, it is much persecuted by the boring stem caterpillar of the moth *Nonagria Typhae*, which in some places has nearly exterminated it.

Platanus (*Platanaceae*).—This genus of trees, the Planes, is of great antiquity, appearing to be abundant in the Cretaceous age, and disappearing from Europe, except the eastern corner, in the Pliocene age. A plant like this, with so great an antiquity and so excellent a provision for dispersal in its light plumed fruits, might have been expected to be as widely spread at least as oaks, which have but a poor system of dissemination, but this is not the case. *P. orientalis* spreads from Eastern Europe to Kashmir. In America there are about 6 species, ranging from the north as far south as Mexico. *P. acerifolia*, the London plane, is a hybrid.

The small obconic 1-seeded fruits are furnished at the base with rather stiff numerous hairs (Pl. X, fig. 5). They are produced in round balls, which break up (in the spring in England) and release the fruits, which are blown away from the tree and along the ground to a very considerable distance, over 150 yards. *P. occidentalis*, *P. Wrightii*, *P. Lindenii* and *P. Mexicana*, of America, are all recorded as inhabiting banks of streams and rivers, which suggests that their seeds are, to some extent at least, dispersed by water after being blown from the trees.

Eriophorum (*Cyperaceae*).—The Cotton grasses are very conspicuous plants in our moorlands, and are widely spread over the north temperate zone and arctic zones of both hemispheres. The typical species have from 1 to 3 or more heads of small nuts surrounded by a number, 20 or more, fine, soft, white setae, very much longer than the nuts, and forming a plume in fruit. *E. alpinum*, *E. Scheuzeri* and *E. capitatum* have a solitary terminal head, and *E. latifolium* and *E. angustifolium* several heads, and are taller plants. When the nuts are ripe they are blown across the moorlands with their silky plumes, and are thus spread to great distances. The silky hairs are the development of the setae or bristles which surround the nut in species of *Scirpus* and allied genera, in which they are too short to be of any value as wind-dispersers (Pl. XI, fig. 2).

It may be noticed that the tall species, *E. latifolium* and *E. angustifolium*, with several heads pendulous on tall stems, are more widely distributed than the shorter stiff-stemmed, single-headed species. They are naturally more exposed to the winds which blow across the moors.

I have seen specimens of *E. angustifolium* from the Transvaal, Jamaica and Cuba, doubtless introduced, as it was formerly used for stuffing pillows and other purposes.

The Cotton grasses may be traced from certain species of *Scirpus*, very chracteristic of the open country of North America. *Scirpus lineatus* has a tall panicle of numerous pendent small spikes. The minute and very light nuts are surrounded by a number of setae little longer than the nut. When a ripe panicle is shaken or blown by the wind, the nuts fly to some distance, distinctly aided by these bristles. Frequently the glume is detached with the nut, and acts also as a wing, increasing the distance of flight. Allied to this North American plant is *S. eriophorum*. Here the setae are very much longer—twice to four times as long as the nut—5 or 6 in number. This plant is more widely distributed, occurring not only in North America, but in temperate Asia to the Himalayas. Closely resembling this in appearance is *Eriophorum comosum*, of India, China and Cambodia. Formerly the last two species of *Scirpus* were put by Bentham under *Eriophorum*, but Clarke separates the two genera by the increased number of bristles, from 20 to 40, or with from 20 to 40 segments, and *E. comosum* has the larger number of bristles. In fact, this suggests the evolution of *Eriophorum* from *Scirpus*, or at least from its section *Sylvaticae* (genus *Seidlia*) by the longer growth of the setae and their being split into numerous slender segments, forming an ideal apparatus for their dispersal by the violent breezes which sweep across the cold and arctic moorlands of the north.

Myzodendron (*Myzodendraceae*).—This genus of parasitic shrubs was formerly classed with *Santalaceae*. They are natives of temperate South America and parasitic, like mistletoe, on trees, *Nothofagus*. When ripe the base of the ovary extrudes 3 slender plumed and viscous filaments which push through the sides of the calyx. They vary in length in different species. Those of *M. linearifolium* are as much as 2 inches long. The fruits are produced in great abundance, so that the plant in fruit is a mass of filaments. They are distributed by wind, and the viscous filaments, which eventually deliquesce, cause the fruits to adhere to any branches they touch. It is suggested also that they adhere to birds, which is probable, but there seems no definite evidence of this, and they seem mostly to be disseminated by wind. The structure of the flying organs of this plant is quite unlike anything else known to me in the vegetable kingdom (Pl. X, fig. 11).

PLUMED SEEDS.

Plumed seeds are always contained in a capsule or follicle, and are generally numerous, small and light, and bear plumes of one to innumerable fine hairs. The plants bearing them are usually tall or moderately tall herbs, climbers or epiphytes, rarely trees.

The capsule is usually linear or lanceolate, more rarely ovate or conic. It may be split on one side only, the sides reflecting or spreading, exposing the seeds, which gradually drift away on the wind, as in *Apocynaceae*, *Asclepiadaceae*, and *Aeschynanthus* (*Cyrtandraceae*), or they may split into 4 or 5 linear lobes gradually from top to bottom, setting free the seeds as they are exposed by the slow splitting and recurving of the valves, as in *Epilobium*. In all cases the escape of the seeds is slow, and often several days elapse before the whole capsule is empty. By this means the seeds are diffused more widely than they

would be if released in a mass simultaneously, especially as the wind in most spots varies in strength and direction every few hours.

The fully plumed seeds, with many hairs, lie in the capsule with the plume compressed, pointing towards the apex, closed and opening widely when released, like a parachute.

Epilobium (*Onagraceae*) is a genus of herbs, sometimes creeping, in which the erect stems are terminated by a raceme of pink or white flowers which open gradually from the base upwards, and are succeeded by long terete linear erect pods containing a large number of plumed seeds. These dehisce slowly from the top downwards, releasing the seeds a few at a time.

The genus chiefly occurs in temperate regions, but is widely spread in both hemispheres into subtropical areas and chiefly in mountainous districts. It is abundant in Europe, North and South America, temperate Asia to India, Australia and New Zealand, rare in Papua, Java and the Philippines, and there are several species in Africa (tropical and South), and one in Madagascar. In distant islands they are usually scarce. Three are found in the Canaries and as many in Madeira. The species are mostly somewhat closely allied, and perhaps many might be condensed, but few definite species are of wide distribution. *E. hirsutum*, common in Europe, occurs in Madeira, India and tropical to South Africa, and *E. parviflorum* occurs also in Europe, Morocco and Azores, Canaries, Madeira and India. There is no reason to believe that either of these have been accidentally introduced by man into the Atlantic islands. Indeed, the only record of any species as being introduced by man anywhere is *E. palustre*, of Europe, introduced accidentally into Rhodesia. These plants, which usually occur in damp spots, by watercourses, etc., can readily be dispersed over land by aid of the plumed seed at a fairly rapid rate, and can go to great distances. As the seeds fly fast, rising on the wind to a considerable height, and cannot be followed, so widely are they distributed over any land area, it seems impossible to rely on the occurrence of specimens at long distances apart. I have, however, a record of a plant of *E. hirsutum*, in Kew Gardens, found at a distance of 300 yards from the parent plant.

E. angustifolium (which with some allied species is often separated from *Epilobium* as a genus *Chamaeneriüm*) is a very well-known plant inhabiting drier places than most species of the genus. It is a herb varying in height from about 3 to 8 feet, with a large terminal raceme of very many flowers, which develop so slowly that the lower capsules are dehiscing and discharging their seed before the uppermost flowers are open. Thus the dispersal of seed from one raceme may last over two months. The capsules are linear and terete, about 8 cm. (4 inches) long and 2 mm. through. They split gradually from top downwards to the base into 4 narrow valves, the whole emptying of the capsule of the seeds occupying some days. There are about 100 seeds in a capsule, and of these, in pods which I have examined, usually only about 3 or 4 are infertile. They are linear oblong, 1 mm. long, smooth, brown, and very light, and bear at the tip a plume of about 50 fine white silky hairs ½ an inch in length. While in the capsule, they remain closely pressed together till the valves are spread and reflected to the point at which the seed lies, when the plume expands widely and the seed sails away.

As during the period occupied in the discharge of the seeds the wind in this country constantly varies in direction, the seeds fly to different points of the compass on different days, and consequently can be spread over a very large area in a short time. The distance to which they are carried by the wind is very great, as, like other species of the genus, they rise to considerable heights. The seed may be brought to the ground by rain or by striking against some object (for the plume is readily detached from the seed), or simply by the fall of the wind, or by drifting beneath trees or in spots

where the wind is ineffective. As in all such plants, a certain proportion of seed falls to the ground speedily, and may grow in the neighbourhood of the parent; but the plant is extremely rhizomatous, and throws up many shoots, which is the main reason that it forms the showy masses of colour which it does in our woods.

The plant is found all over Europe, as far north as Iceland, and to North India, China, Japan and North America. Its distribution is perhaps not so wide as that of *E. hirsutum*, a wet-loving plant, probably because it requires rather special localities for its growth. It is well known that it specially loves to grow in newly-felled forest, in the open spaces formed by clearing, and during the Great War, when so many woods were felled, it soon became very conspicuous, covering the ground with a pink carpet which could be seen from a long distance. As, however, the destroyed vegetation returns and shades the plants, they get smaller and eventually disappear again. As it is a popular plant in cultivation, its seeds often escape from gardens, and this is the source of the plants which spring up in and around London, where it may be seen growing freely between the lines of the abandoned part of the District Railway between Hammersmith and Turnham Green.

Tamarix.—The Tamarisks are shrubs with small capsules containing minute seeds terminated by a plume of hairs long enough to carry the seeds to some distance by the wind.

Myricaria is similar, but has capsules and seeds much larger. Both genera are found in deserts, seashores and open country and along rivers, in Europe, temperate Asia to China, Arabia, India, tropical Africa. Two species of Tamarisk, *T. gallica* and *T. anglica*, occur in the Canaries, and the former in Madeira and the Cape Verdes. Troup states that the seed of T. *gallica* is dispersed, not only by wind, but also by water. Like most of the wind-dispersed plants, the seed is able to float, and perhaps it is in this way that it has reached Madeira and the Cape Verdes. To the same order belongs *Hololachne*, a dwarf shrub of the deserts of Yarkand, in which the seeds are hairy all over, but the hairs are not longer than the seed, and certainly are not capable of acting as flying apparatus; and *Reaumuria*, of the deserts and sand-dunes of Sicily, Algiers, Palestine, Egypt and Arabia, in which the seed is terminated by a stiff tuft of hairs not long enough to carry the seed through the air, though they certainly might help to drift the seed along the sand when the wind was blowing. It will be noticed that the *Tamarisks* and *Myricaria*, with their very small well-plumed seeds, have a much wider area of dispersal than the more primitive *Tamariscineae*, *Hololachne* and *Reaumuria*.

Apocynaceae.—This order attains its largest development in the tropics of both worlds, but some species occur in the warmer parts of the temperate regions. They are mostly shrubs, often climbing, and small trees, more rarely big trees or erect herbs.

The section *Echitideae* consists of plants, almost all of which have plumed seeds, and there are a few genera among the *Plumerieae* which also have plumed seeds, but most of this section and the remainder of the order have the fruit in the form of berries or drupes, or if follicular, the seeds are winged. The ovary of these plants is formed of two carpels, which in the capsular fruits develop into a pair of long cylindric pods, more rarely lanceolate in outline, which dehisce on one face, allowing the seeds to escape. In some of these capsular fruits the seed is narrow oblong, with an oblong blunt wing at each end, and these narrow wings in many cases have evolved into a plume of silky hairs at one end or the other, rarely both.

Malouetia, a small genus of South American and African trees, may be taken as one of the primitive plants leading up to the plume-seeded *Apocynaceae*. The seeds are elliptic and covered entirely with hairs pointing upwards. Though

the hairs are comparatively short, they may play some part in drifting the seeds away from the parent tree to some distance in the wind.

The next stage is represented by the genus *Alstonia*, lofty Asiatic trees reaching to over 100 feet tall, and, indeed, among the tallest trees in the order. These have long slender pods, dehiscing along one face, and containing a number of short oblong seeds, shortly hairy on the faces and with two tufts of long hairs, one at each end, while the sides are also edged with long hairs. The pods are usually about 12 inches (30 cm.) long, and quite slender. In *A. neriifolia*, of China and Bhotan, the whole seed is hairy. In *A. scolaris*, *A. venenata* and *A. spathulata*, Asiatic trees of some size, the seed is glabrous except for the tufts of hairs at both ends and along the edges. The seed in most of these is about ⅓ inch long, and the plume or tuft of long hairs at each end is just as long. In *A. villosa*, of Fiji Islands, the seed, which is 5 mm. long, oblong, hairy on the edge, is drawn at both ends into equally long points, which are feathered with hairs.

The greater number of the species of *Alstonia* are natives of the forests of India, China, the Malay Peninsula and islands, including Timor, and there are several in Australia and Polynesia. The species *A. villosa*, of Fiji, also occurs in Cook Islands. Guppy (" Naturalist in the Pacific," 384) writes :—
" Besides possessing, in Samoa and Fiji, peculiar species, the islands of Western
" Polynesia have in *A. plumosa* a species common to Fiji, Samoa and New
" Caledonia. Another species, *A. costata*, is restricted to Eastern Polynesia,
" occurring in the different islands of the Tahitian group, as well as in Raratonga.
" The long ciliated or hairy seeds, 6 to 9 millimetres in length, are fitted for
" transport by the winds and in birds' plumage. It is probable that the thick
" white juice (latex) oozing from a broken branch would at times add to the
" adhesion to a bird's feathers."

This may perhaps occur, and account for the transportation of the seeds by birds over the Polynesian group and to other islands, but there can be no doubt that the main dispersal of seeds over the great area occupied by these trees is due to the action of the wind blowing seeds from the long pendent pods, dehiscing on the tree, to some considerable distance. I have frequently seen this in *Alstonia angustiloba*, a very large tree in Singapore.

Two species (of which I have seen no fruit) are found in tropical Africa, and one with seeds resembling those of *A. villosa* occurs in Costa Rica. From the seed tufted at both ends, as illustrated by *Alstonia*, it is an easy transition to the seed tufted at one end only and with a much more elongated plume of silky hairs, so that the plumed seed resembles the plumed fruit of the *Composite*, and flies to long distances in the wind. As in the *Composite* plumed fruit, the seeds are very easily detached from the plume, and when the flying seed strikes against an obstacle it is readily detached, so that it may be deposited at the edge of a forest or at the base of a tree, where, should it be a climber, as so many of the *Apocynaceae* are, it would fall in a suitable place for its future growth. In the greater number of the section *Echitidae*, which are mostly climbing shrubs, some (*Beaumontia*, *Urceola*, *Choneomorpha*), however, being very big lianes, the organ of flight is a simple long tuft of hairs, up to as much as 3 inches long, on the tip of an oval or lanceolate, flattened thin seed. The seed itself is usually glabrous, or only slightly hairy, but in the Oleander (*Nerium*), a tall shrub on river banks and open country in temperate or subtropical Asia, the seed is short, about ¼ inch long, and entirely fluffy, with a plume about as long as the seed—in fact, these seeds may perhaps be considered intermediate between those of *Malouetia* and those of typical *Echitidae*.

In the whole section of *Echitidae* the seed is plumed at the upper end, except in the genus *Kickxia*, where it is plumed at the base. In the greater number of species the seed is oblong, linear or ovate, and narrowed at the tip,

on which is borne the plume, a large tuft of hairs, silky and considerably longer than the seed. In *Strophanthus*, a genus of bushes, sarmentose shrubs, or big lianes met with in tropical Asia and Africa, the seed is prolonged into a long slender point feathered on all sides. In *S. Emini*, a big African liane, the silky lanceolate seed is 1 inch long, the beak, very slender, is 5 inches long, the lower 2 inches are bare, the remainder feathered with hairs 1 inch long, spreading in all directions. In *S. hispidus* the beak is feathered to the base and shorter (Pl. XI, fig. 4, *S. Preussii*).

Kickxia (1 Javanese and 1 African species) has a long feathered beak, 4 to 6 inches long, from the base of the seed. These are big trees.

The genus *Parsonsia* is rather more widely distributed than most of the other *Echitidae*, *P. spiralis*, a slender climber, occurring on sea coasts all over tropical Asia up to Formosa. This plant seems always to grow on sandy seashores, and I note that the seed has a corky testa. It is probable that it is partly dispersed by sea, into which its seeds are blown. The inland species have no corky testa.

The *Asclepiadaceae* in their fruit and seeds closely resemble the *Echitidae*. They have the same pair of pods, long and narrow, or ovate or lanceolate, splitting along the upper face and emitting oblong or ovate seeds bearing a plume of hairs on the top. The only exceptions are *Finlaysonia* and *Sarcolobus*, tidal mud plants, the former of which has an oblong seed covered with hair pointing to the tip and somewhat longer there, and the latter being quite glabrous. These seeds are distributed by river action only. The *Asclepiadaceae* are shrubs or climbers, usually slender, rarely herbaceous, and occur in hot open country, mostly in the tropics, more rarely in temperate regions. *Dischidia* and some allied species are strictly epiphytic, as are some of the *Hoyas*. In the case of *Dischidia* there is reason to believe that ants play a considerable part in their distribution, and such information on this as is available is given under Dispersal by Insects, *see* p. 526. Except for some *Dischidia* on the exposed branches of high trees, *Asclepiadaceae* are absent from the dense forests. They are by no means common in oceanic islands. There are a considerable number in Socotra, *Ectadiopsis* (2), *Mitolepis*, *Cochlanthus*, *Secamone*, *Echidnopsis*, *Edithcolea*, *Vincetoxicum*, *Daemia* (1 each), *Glossonema* (2), and *Sarcostemma* and *Bucerosia* (3 species). The nearest coast, Africa, is rich in these plants, and it must also be considered probable that Africa was formerly in actual land connection with Socotra. In Fernando de Noronha there is 1 endemic species of *Gonolobus*, *G. micranthus*. I found that the Tyrant bird *Elainea Ridleyana* lined its nest with the plumes of the seed of this plant, and it may have been brought over from Brazil by attachment to the feathers of some such small bird. An endemic species of *Hoya* occurs in Christmas Island. The *Hoyas* are usually climbers on trees in open places, especially on the seashores. They are found abundantly in India, the Malay Peninsula and islands, in Australia and the South Pacific, Polynesian Islands. It is not improbable that *H. Aldrichii*, of Christmas Island, or its ancestor, was brought by a bird, as suggested for *Gonolobus*.

Cynanchum Blumei arrived at Krakatau by 1906, 20 years after the flora had been destroyed by the eruption. *Periploca laevigata*, a Moroccan and South European and Palestine plant, occurs in the Canaries, as does an endemic plant, *Ceropegia dichotoma*.

A few widely distributed species owe their great area of dispersal to man. Such are 2 species of *Calotropis*, of which the plumes are used for stuffing pillows and the plant itself as a drug, and *Asclepias curassavica*, an American plant, now scattered all over the warm parts of the globe and readily spreading along roadsides, and which is now found in the Canaries and Polynesian Islands, Fanning Isle, Rurutu, and in Little Kei, etc., introduced on

account of its handsome red and yellow flowers, and formerly valued as a drug.

Gomphocarpus fruticosus is found in Madeira and the Canary Islands, and also in Australia (1844), apparently always a garden escape. It is a native of Southern Europe and Morocco.

The comparatively feeble insular dispersal of *Apocynaceae* and *Asclepiadaceae*, compared with other plumed fruits and seeds, seems to me probably due to the larger and consequently heavier seed, and to the comparatively scarcer occurrence of the two orders.

Aeschynanthus (*Cyrtandraceae*), together with some allied plants, possesses a simple flight organ in the form of 1 or 2, or occasionally more, hairs from one or both ends of the minute seed. The plants are epiphytic, or more rarely rock plants, natives of tropical Asia. The capsules are very long, slender and cylindric, usually pendent, often 6 inches long. They dehisce on one side only, exposing a very large number of minute elliptic pustular seeds, of which the testa is drawn out into a long slender thread-like hair covered with scattered short processes. In some cases, in *Dichotrichum* and *Agalmyla*, one of these hairs is split at the tip, and in *Aeschynanthus longicaulis*, of India, and *A. Motleyi*, of Borneo, there are from 30 to 40 hairs at the hilum of the seed, 12 mm. long, and one terminal hair, 18 mm. long. *Lysionotus* and *Loxostigma*, which grow on banks, rocks and old tree trunks, have 1 hair at the top of the seed and the funicle long drawn out to resemble a hair at the base, which suggests that the basal hair in *Aeschynanthus* is derived from the funicle. Most of the seeds, if not all, are papillose or covered with very minute scales. The seeds of *Aeschynanthus* curiously resemble those of the epiphytic species of Malayan *Rhododendrons*. The advantage of these long slender hairs and their short processes, and also the scales or papillae on the body of the seed, to epiphytic plants is obvious. If the seed were not armed with these hairs, they would fall to the ground beneath the tree on which the epiphyte is growing. By this arrangement the seed is borne on the wind from tree to tree or branch to branch, and adheres to the bark by the processes on the hairs and the seed (Pl. III, fig. 8, Pl. XI, fig. 7).

The distance of flight of *Aeschynanthus* and its allies does not seem very great, as these plants are absent from most islands in their area, but 2 species of *Aeschynanthus*, *A. pulchellum* and *A. volubile*, had reached Krakatau by 1919.

Tillandsia (*Bromeliaceae*) and its allies, *Guzmania*, *Calopsis*, *Caraguata*, have rather curiously plumed seeds. They are very light and small, linear, with the testa drawn out into a short point at the tip and a long one at the base. The latter breaks up into long silky hairs, by which the seed is borne away in the wind (Pl. XI, fig. 6). In *Tillandsia recurvata* the seed is 3 mm. long, and the plume at the base 15 mm. In *T. bulbosa* the seed is 4 mm. long, the apical process 5 mm., and the basal plume 40 mm. long. The capsules, in a raceme or spike, split into 3 valves from the top, and in dry weather in some species the base twists like a corkscrew, helping to eject the seeds.

Many other species of the order have wings or crests on the seed, but only the *Tillandsiae* have them developed into plumes. The whole order is confined to America, chiefly tropical South America, ranging as far north as Florida. The genus *Tillandsia* is the most widely distributed, and 1 species occurs in Galapagos and 1 in Cocos Island, about 500 miles from South America. The species are all epiphytic. The seeds, drifting on the wind, become attached to the bark of a tree on touching it, so it is said, by the terminal point. It is not uncommon in Jamaica to see small plants growing on the telegraph wires by the roadside. *T. usneoides*, "Spanish moss," is said also to be dispersed by portions of the branches being blown off upon other trees and adhering thereto, where they grow readily.

A rather curious case of seed plumed at both ends occurs in *Amphicome*, a small genus of *Bignoniaceae*, 2 species of which are found in India and China. Except for these plants, the remainder of the numerous species of the order which are wind-dispersed have winged seeds. There are, however, a few *Bignoniaceae* which have unwinged corky seeds, and some which have baccate fruit, and small seed unprovided with any apparatus for wind-dispersal. Most of the species allied to *Amphicome* have seeds with a linear or oblong wing at each end of the seed. It is these terminal wings which in this plant are converted or modified into a tuft of fine silky hairs at each end of the small seed. The pods, which are long and cylindric, contain many of these plumed seeds, and dehisce by a central line down one side, as in the case of the *Asclepiadaceae* and *Apocynaceae*. *Amphicome* is a herbaceous plant with a more or less woody base, about 1 foot or more tall, and inhabits rocky places. It is almost the only genus of herbaceous plants in the order, and the low height of the pods from the ground is probably correlated with this modification. It should, however, be mentioned that the equally low herbaceous *Incarvillea*, of China, retains the typical winged seed of the order, but it may be noted that the plume-seeded *Amphicome* is more common and more widely distributed than the local and scarce *Incarvillea*.

Woolly Seeds.—In these the seeds borne in a dehiscent capsule are covered with short woolly hairs all over, sufficiently long to allow the seed to be wind-dispersed. A certain number of seeds in capsules are more or less hairy, but they are not common, and, except in the following cases, are not long enough to assist in dissemination at all. In one case, *Barclaya*, a Water-lily, the seeds are covered with hooked hairs which are adhesive to wild pigs.

As in the case of thistledown, the woolly hair of these seeds is sometimes freed from the capsule without seed being attached, and may fly on the wind to a great distance. This is due to the ovule being unfertilised and not developing, and is not uncommon in the case of unisexual trees, as in *Salix* and *Populus*. In these, if there is no male plant in the vicinity, the seeds are not developed, and on dehiscence of the capsules the wool, with only the perished ovule attached, flies away and may be scattered over the country. It is therefore necessary, in recording the distance of flight in such trees, to see if there are any ripe seeds attached to the flying wool. I have seen the ground white with wool from *Populus nigra* in Kew Gardens, not only round the tree, but blown to a great distance, and drifting along through the air like snowflakes, but was quite unable to find a single good seed among the wool. Of course, wool without seed, being lighter, will fly much further than the seed-bearing wool. These woolly-seeded plants are nearly altogether absent from remote islands, but perhaps this is due rather to their being few in number than to the capability of flight of the seeds.

There are a few species of *Salix* in Iceland, and *Salix canariensis* occurs in the Canaries and Madeira, but these islands are almost certainly continental. The arctic Sallow seeds may be blown into and across ice, and so widely spread from island to island.

The woolly-seeded *Malvaceae* are *Bombax*, *Ochroma*, *Eriodendron* and *Gossypium*. All but the last are big trees, from 40 to 60 feet tall, and are usually found in open country, savannah lands, but I have seen *Bombax* in the Malay Peninsula in forests. The capsules open into 4 valves and release the seeds (which are often very small with long wool) gradually.

Ochroma, of the West Indies and South and Central America, *Bombax* and *Eriodendron*, frequently produce the fruit when the leaves are fallen, so that the seeds are well exposed to the wind. In *Eriodendron* the pods are long pendent below the branches. *Bombax* occurs in Africa, India, Siam, Cochin China, the Andamans, the Malay Peninsula (scantily), Sumatra, Java, Timor

Laut and North Australia, and Central and South America. Troup (in his "Sylviculture") says that the seeds of *B. malabaricum* in their wool may be blown for many miles. The seeds weigh from 750 to 900 to the ounce, while those of *B. insigne* are heavier, and only from 330 to 570 go to an ounce. Perhaps it is due to this difference in weight that *B. malabaricum* is more widely distributed than is *B. insigne.*

Bombax malabaricum var. *polystemon* occurs in Narcondam, an endemic variety. *B. malabaricum* occurs in the Andamans, and *B. insigne* is reported by Kurz for the same islands. King, however, thinks that this plant is an undescribed species also met with in Cocos Island, Andamans, by Prain. The Andaman Islands were probably connected with the mainland of Tenasserim at one time, but the Narcondam plant seems really to have crossed the sea by air.

Eriodendron anfractuosum (the Kapok) is found in West Africa as a very large tree, but is not a big one in most places. It occurs in the Cape Verde Islands, India, Andamans (small tree), Siam, Malay Peninsula (cultivated), Java, Philippines, Madagascar and Comoro Isles, but in many of these places it is introduced for its valuable wool. Other species occur in Mexico, the West Indies, and South America (Pl. XI, fig. 8.)

Gossypium is a low shrub or small tree. The cotton is now cultivated all over the world where it is possible to grow it. The seeds drift in the wind when the pod dehisces, but it does not appear to spread rapidly anywhere.

Cochlospermum (*Bixineae*) is a shrub about 5 feet tall, with woolly seeds, the wool in *C. tinctoria* being about 1 inch long. It occurs in Africa and India, and has been introduced into Penang, where it has spread a little about the town. Two or three species are found in Australia and some in South America.

Calantica and *Bivinia* (*Samydaceae*) are trees of Madagascar with small, round oval capsules opening at the top into 4 valves. The seeds are very small and covered with long woolly hairs, evidently an evolution from the testa. They are not so woolly as those of the Cotton trees, and the hairs are less abundant, but doubtless they aid in the dispersal of these local plants.

The Willows and Poplars (*Salix* and *Populus* (*Salicaceae*)) are inhabitants of the north temperate regions. *Salix* is found in the Arctic regions, all the temperate regions of Europe and America, and descending to the tropics in India, Java, Sumatra, Philippines, Africa, Madagascar, South America, but absent from all other tropical islands, the Malay Peninsula, Australia and Polynesia. One species occurs in Madeira and the Canaries (*S. canariensis*), and several in Iceland. *Populus* (bigger trees than *Salix*, which often in Arctic regions are very low creeping shrubs), is found in the north temperate region, India and Africa, and in America as far south as Mexico. In these plants the capsule, which dehisces along the upper surface, contains a number of seeds, each enveloped in a tuft of silky fibres from an outgrowth of the funicle. As most of these are open-country or river-bank plants, the woolly seed is blown away to a long distance.

A. W. Williamson (in "Cotton-wood in Mississippi Valley") says the seeds of the Cotton-wood (*Populus deltoides*) are often carried miles by the wind and by overflow waters, which frequently leave fertile seed on the muddy alluvial flats far from the parent tree. Seeds three weeks old have a germination of 50 per cent.

Troup (in "Sylviculture") says of *Populus ciliata*:—"The silky down "round the minute seeds forms a protective covering, preventing the seed "from being washed away, and retaining moisture."

I found rather a curious method of dispersal of the Willows, *Salix alba* and *S. fragilis*, along the banks of the rivers Thames and Kennet, near Reading. Very large numbers of spikes of the fruit of these trees drifted down the river

PLATE XI.

WIND-DISPERSAL. PLUMED AND WOOLLY SEEDS AND FRUITS.

FIG. 1.—*Imperata exaltata* (spikelet, enlarged).
,, 2.—*Eriophorum angustifolium* (achene plumed, enlarged).
,, 3.—*Phragmites communis* (spikelet, enlarged).
,, 4.—*Strophanthus Preussii* (seed).
,, 5.—*Stipa pennata* (spikelet).
,, 6.—*Tillandsia vestita* (seed enlarged, after Schimper).
,, 7.—*Aeschynanthus ramosissimus* (seed enlarged, after Schimper).
,, 8.—*Eriodendron anfractuosum* (fruit and woolly seed).

[*To face p.* 158.

with the capsules not dehisced. On being drifted up on the banks, when they became dry the capsules dehisced and released the woolly seeds, which were blown along the banks of the river by the wind, so that these plants have the double advantage of being dispersed by wind and water.

Wallace (" Darwinism," p. 379) gives an account of a vast flight of plumed seeds communicated by Thomas Hanbury from Shanghai, May 1st, 1856 :— " This morning myriads of small white particles are floating about in the air. " There is not a single cloud and no mist, yet the sun is quite obscured by them." The plumes were identified by Mr. Hemsley as those of a *Populus* or *Salix*. The amount of seed that one of the Poplars produces in the season is very large, but, owing to their being unisexual trees, it often happens that the fluff produced in such large quantities is seedless.

PLUMED FRUITS AND SEEDS IN OCEANIC ISLANDS.

The occurrence of plumed fruits and seeds in distant islands is of some importance as showing the distance that these plants can travel through the air. In continents a plumed fruit or seed may, when it comes to rest, be blown further along the ground, but in crossing the sea the fruit or seed is lost when it descends ; it cannot rise again, nor drift further. In giving this account of this class of fruit or seed in the oceanic or distant islands, the possibility of the seeds being attached by their plumes, by viscidity or by retentive hairs to the plumage of a bird, and so borne to the island, must not be lost sight of. We know that this can take place, and probably often does. The occurrence in White Island, near New Zealand, of *Sonchus oleraceus* in the haunts of gannets is almost certain to be due to its having been carried by the birds. In Fernando de Noronha the plumes of the seed of the only plume-seeded plant there—*Gonolobus*—is used by the endemic Tyrant bird (*Elainea Ridleyana*) to line its nest, and it or its ancestor may have been brought attached by the plumes to the original *Elainea*.

I have excluded from these lists all plumed fruit or plume-seeded plants which might, and, indeed, in most cases certainly have, been transported by man, such as *Sonchus oleraceus*, *Taraxacum*, *Vernonia cinerea*, *Asclepias curassavica* and *Calotropis* (though, in some cases of these fellow-travellers with human beings, the plants have continued their voyages by a natural means), the object being rather to show to what distance across the sea these flying fruits and seeds can travel.

In the following islands no plants of this class are known to occur at all :— Ascension, Marion Isle, Crozets, Kerguelen, Heard Island, St. Paul, Amsterdam, Admiralty Islands.

Iceland, 250 miles from Greenland, its nearest land. It is by no means certain that this island was not formerly connected with the mainland and derived its flora thence. We must also allow for the transport by or across ice, and also it has been inhabited for many centuries. There are *Epilobium* (8 species), *Dryas*, *Valeriana officinalis*, and about 17 *Compositae*, including *Taraxacum* and *Sonchus*, and *Salix*.

Azores, 900 miles from Portugal and 550 miles from Madeira, have *Epi obium parviflorum* and (*Compositae*) *Galactites tomentosa*, *Solidago sempervirens* var. *Azorica*, *Senecio malvaefolius*, *Tolpis* (4 species), 1 also a native of the Canaries, and 2 South European, *Thrincia nudicaulis*, also in Madeira and the Canaries, *Picris* (2 species), and a number of plants certainly of human introduction.

Madeira, 450 miles from Morocco, 42 plumed *Compositae* of the genera *Conyza*, *Filago*, *Carduus*, *Cirsium*, *Silybum*, *Tolpis* (3), *Crepis*, *Andryala*, *Hypochaeris*, *Lactuca*, *Sonchus* (3), *Tragopogon*, *Urospermum*, and a good many of obvious human importation.

Canaries, 50 miles from Cape Juby, *Epilobium* (5 species), (*Compositae*) *Erigeron*, *Conyza*, *Filago* (5), *Phagnalon* (5), *Gnaphalium* (1 endemic), *Schizogyne*, *Viraea*, *Artemisia* (3, 1 endemic), *Senecio* (17), *Kleinia*, *Carduus* (5), *Silybum*, *Tolpis* (6), *Barkhausia* (3), *Andryala* (2), *Hypochaeris*, *Thrincia*, *Lactuca*, *Picridium*, *Sonchus* (17), *Urospermum*, *Microrhynchus*, also *Periploca*, and an endemic *Ceropegia* with African coast affinities (*Asclepiadaceae*), *Typha angustifolia*, and *Salix canariensis* (*Salicineae*).

Both Madeira and the Canaries, it is believed, were continental islands, a prolongation of the North African coast having been cut up by the sea into detached islands. The flora is distinctly continental in type. Both contain a number of endemic species, but there are a good many *Compositae* of human importation, and some in the above lists may have been so introduced.

Cape Verde Islands, 500 miles from Senegal, have *Compositae*, *Erigeron* (2), *Conyza* (4), *Phagnalon* (2), *Blumea* (2), *Pluchea* (1), *Artemisia*, *Gnaphalium* (2), *Tolpis*, *Urospermum*, *Lactuca*, *Sonchus*, *Microrhynchus* (2); *Asclepiadaceae*, *Periploca* and *Sarcostemma*.

Chagos.—The only *Composites* on this island are *Vernonia cinerea* and *Ageratum conyzoides*. Hemsley puts them in the list as not introduced by man, but the latter is most extensively dispersed by man, and the former frequently so.

Maldives, 350 miles from Cape Comorin and 400 miles from Ceylon. Trimen gives *Launea pinnatifida* and *Calotropis procera*, *Blumea membranacea*, *Emilia sonchifolia* and *Lactuca polycephala*.

Laccadive Islands, 120 to 180 miles from India, have *Vernonia cinerea*, *Crepis acaulis*, *Launea pinnatifida*, *Calotropis procera*, *Cynanchum alatum*, *Tylophora*. Prain thinks the last 3 *Asclepiads* may have been introduced, and Willis and Gardner say that *Calotropis* is cultivated in all villages. The *Launea* is apparently sea-dispersed (see under that section), and it seems probable that the rest of the plume-fruited plants *Compositae* are also introduced.

Minikoi has only *Vernonia cinerea* and the *Launea*.

Narcondam and Barren Isle.—The first island is 80 miles from the North Andamans and 74 miles from Barren Island, which is 60 miles from the North Andamans. They have *Bombax insigne* var. *polystemon* (a local variety), *Vernonia divergens*, *Blumea glomerata*, *B. laciniata*, *B. myriocephala*, *Pluchea indica*; *Tylophora globifera*, *Hoya parasitica*, *H. diversifolia*, *Dischidia nummularia*; and the grasses *Pogonatherum saccharoideum* and *Thysanolaena acarifera*, both also in Barren Island. Prain suggests the latter seed may have come by wind, but the spikelets are not plumed. Undoubtedly some of these plants, especially the *Asclepiads*, *Blumea myriocephala*, and the *Bombax*, were wind-borne. The distance from the Andaman Islands is not very great, and we know from more remote islands that seeds of *Blumea*, *Hoya* and some other *Asclepiads* have travelled further than that (Christmas Island, Fernando de Noronha).

Christmas Island, 194 miles from Java, 1 *Hoya*, 1 *Composite*, *Blumea spectabilis*, the grass *Ischoemum nativitatis* (this grass is drifted about by the wind here, but I am doubtful that it can have arrived by wind).

Krakatau, 25 miles from Java. All Javanese species. *Compositae* (8), *Blumea* (2), *Erigeron linifolius* (*E. sumatrensis*), *Emilia sonchifolia*, *Erecthites hieracifolia*, *Pluchea indica*, *Senecio* (1), *Vernonia cinerea*; *Asclepiadaceae*, *Cynanchum Blumei*; grasses, *Imperata arundinacea*, *Pennisetum macrostachyum*, *Phragmites communis*, *Pogonatherum crinitum*, *Saccharum spontaneum*.

Cocos-Keeling Islands, 700 miles from Java, *Sonchus oleraceus* and *Vernonia cinerea*, both probably accidentally introduced by man.

Auckland Isles, 180 miles from New Zealand, *Compositae*, *Ozothamnus Van Villersiae* (also in New Zealand and Campbell Island), *Pleurophyllum* (2 species), and *Celmisia* (1 species) (in these species the pappus is rigid and suggests adhesion rather than air transport).

Macquarie Isles, 600 miles from New Zealand, *Pleurophyllum criniferum*.

Juan Fernandez, 400 miles from Chile, *Compositae*, *Erigeron* (2), *Gnaphalium* (3), (these probably introduced), *Dendroseris* (8), endemic.

San Ambrosio and San Felix, 450 miles from Juan Fernandez, *Lycapsus* (1), *Dendroseris* (1).

Galapagos and Cocos Isle, 600 miles from Ecuador, Cocos Island 300 miles from Costa Rica, nearly halfway between Galapagos and the mainland. *Compositae*, *Aplopappus* (1), *Baccharis* (2), *Brickellia diffusa*, *Erigeron* (1), *Eupatorium* (3), *Perophyllum* (1), and *Gnaphalium luteo-album* and *Sonchus oleraceus* (introduced), *Asclepiadaceae* (2), *Bromeliaceae* (2).

Bermudas, 580 miles from North Carolina, *Compositae*, indigenous (7), *Eupatorium macrophyllum*, *Erigeron Darrellianus*, *Baccharis* (1), *Pluchea* (3) *Solidago sempervirens*. The first 2 species are extinct. The *Solidago* is a salt marsh plant occurring in Florida and the Azores. The *Plucheas* are also maritime, possibly sea-dispersed. The first botanist there was H. May, in December, 1593, and some cultivation had been made even then. All these plants have North American affinities.

Socotra, 500 miles from the Arabian coast, whence the flora is probably derived, and to which it was probably connected by land. *Tamarix gallica*, (*Compositae*) *Achyrocline* (2 species), *Vernonia* (3 species, including *V. cinerea*), *Conyza*, *Heterochaena*, *Launea* (1), *Helichrysum* (several), *Senecio* (1), *Dicoma* (2), *Lactuca* (3), *Psiadia* (1) (possibly adhesive), *Pluchea* (2); *Apocynaceae*, *Socotora*, *Adenium* (6), *Asclepiadaceae* (15), all Africa, 1 from the Canaries.

St. Helena, 1,140 miles from Africa, 1,800 from South America, 698 miles from Ascension, *Commidendron* (4), *Melanodendron* (1), *Petrobium* (1), *Senecio* (2).

Tristan d'Acunha, 5,520 miles from South America, *Chevreulia*, 1 species from Chile and Montevideo, and 1 *Gnaphalium*, of which the achene is rough and may be adhesive. *G. luteo-album*, probably diffused by adhesion to sea-birds, also occurs.

South Trinidad, 600 miles from Brazil, *Achyrocline* (1), perhaps allied to a Brazilian one, may perhaps be adhesive; the pappus is short and the achene scabrid.

Fernando de Noronha, 200 miles from South America, 1 *Asclepiad*, *Gonolobus*; no indigenous plumed *Compositae* or grasses.

Taking the dispersal of plumed seeds and fruits in the islands all round, it seems quite clear that such fruits and seeds can cross the sea for a distance of 400 miles and probably much more.

The Composites *Commidendron* and *Melanodendron*, of St. Helena, are, it appears, more nearly allied to *Diplostephium* and *Olearia* of the Antarctic regions, New Zealand and South America, the distance of which from St. Helena is about 1,000 miles.

In Tristan d'Acunha there was found by Thouars, in 1793, the little creeping Composite *Chevreulia stolonifera*, only otherwise known from South America, its nearest point being Montevideo, a distance of over 5,500 miles, where it grows in swamps, fields and sandy hills. Except *Nertera*, bird-dispersed, and *Lagenophora*, a Composite with adhesive achenes unplumed, it is the only plant

in the island with a distinct affinity with the South American flora, all the others being Australian or New Zealand types. Thouars at the time of his visit found no plants on the island which could have been introduced by man. It does not seem at all probable that the *Chevreulia* was borne to the island adhesively by a bird, as there is no record of any South American bird visiting the island except the wandering sea-birds, and they would not frequent the American sand-hills and swamps. The achenes of the plant are very small, with a long slender beak to the terminal spreading pappus. The involucre of the head, when the fruit is ripe, spreads widely and then reflexes, exposing the extremely light fruit to the faintest gust of wind. I have observed in plants on the rockery at Kew that they fly off from the receptacle remarkably soon and readily, and drift out of sight at once. There is also in the island an endemic species of *Gnaphalium*, a genus of very wide distribution, in which it is quite possible that adhesion to a bird's feathers may at least play a part in their dissemination. The winds blow violently to Tristan d'Acunha from the south and west, i.e., from the direction of America. A few of the ferns there are South American, but most are Australasian and South African. Doubtless the spores of the South American ferns were brought across by winds from the west, and probably the achenes of *Chevreulia* came in the same way. While there is no doubt that the Antarctic islands to the south of Tristan d'Acunha extended further north and occupied a larger area at one time than they do now, and the dispersal of seeds from the southern region may have been by this means more readily effected, there seems no doubt that the island was never connected by land, or by scattered intermediate islands now vanished, with South America. If this little plant reached the island by the flight of its achene from South America, it is the longest flight of a plumed fruit which we have on record.

Another plumed Composite which has nearly as long a flight-distance is *Solidago sempervirens*, a North American and Bermuda plant, of which there is a variety (*Azorica*) in the Azores, a distance of about 1,400 miles from Bermuda. The achenes of this plant must apparently have been brought by wind. We have no record of American birds visiting the Azores, and as it is a distinct variety, it is most improbable that the species was introduced by man from America and altered since, and it is not likely that it arrived on driftwood.

It is quite clear that though we have occasional instances of plumed fruit and seeds travelling by air to very considerable distances safely without descending to sea-level, the further off the island is from the mainland, the fewer can get there. The contrast is very marked between Krakatau, 25 miles, 13 species; Christmas Island, 194 miles, 2 species; Cocos-Keeling, 700 miles, none. The plumed Composites and Asclepiads fly furthest. Grasses evidently fly a shorter distance, the furthest record we have being *Poganatherum*, in Barren Island, 60 miles from the Andamans.

The wind plays an immense part in disseminating Orchid seeds and spores of *Cryptogams* to very great distances, but plumed fruit and seed are practically unable to cross considerable tracts of sea, obviously falling into it after the flight of a comparatively few miles. The plume-fruited and seeded plants are continental, mostly herbaceous, and so, quickly fruiting, can cross over mountains, plains and deserts with great rapidity. If they fall on land, the following blasts of wind can pick them up and carry them on, whereas if they fall into the sea they are lost. It is on the plains of South Africa, the prairies of North America, the deserts of Australia, and such places, that the plants with plumed seeds and fruits are found in greatest abundance. They are scarce or wanting in dense forests and oceanic islands.

CHAPTER II

DISPERSAL BY WATER

FOREWORD.

THE action of water in the diffusion of plants about the globe is perhaps even more important than the action of wind. Like that factor in dissemination, it is one of the earliest and perhaps the most primordial of methods for transportation of fruits and seeds, and for covering the land with vegetation. The earliest plants were probably aquatic and necessarily water-dispersed. Seeds, spores, bulbs, rhizomes and other fragments of the vegetative parts of plants can be carried by rain-wash, rivers and floods all over the continents, and by sea-currents from one continent to another and from one island to another.

The modifications of fruit or seed for water-dispersal are not so elaborate and striking as those requisite for wind-dispersal. Any fruits or seeds light enough to be wind-transported may be dispersed by water, their limit being reached when they absorb so much water that they become water-logged, decay, and sink, or their germinating power is destroyed by the infiltration of water, or again when, having begun to germinate, they have failed to reach a suitable locality for further growth. Many seeds successfully dispersed by river usually sink, or fail to establish themselves when the salinity of the tide reaches a certain point. Almost the only requirements of a seed or fruit for water-dispersal are sufficient buoyancy and a sufficiently long period of impermeability by water to allow of its being drifted as far and no farther than is necessary. The rapidity or slowness of the absorption of water by a buoyant fruit or seed is really the most important factor in successful dispersal.

Millions of seeds are carried down rivers all over the world, often drifting away to the open sea, where they form great masses of sea-drift, mixed with logs and branches of trees. Except in the case of seeds or fruits modified for dispersal by sea, all perish before they can reach a suitable habitat where they can establish themselves. All seeds or fruits light enough to be dispersed by wind are sufficiently light to float in water, but those of inland species have the necessary faculty of absorbing water rapidly for germination, and the greater number are soon destroyed by prolonged immersion. Occasionally we get winged or plumed fruits which can also be dispersed by water, as in *Gyrocarpus* and *Salix*, but usually a wind-dispersed seed or fruit fails to make a successful migration by water.

It does not follow, however, that fruits or seeds actually too heavy to float in water, and which sink soon after they fall in, cannot be effectually dispersed by the action of water. Both large and minute seeds are frequently disseminated by rain-wash or sudden rushes of water over the ground. Heavy seeds may be carried along in shallow waters and washed up with silt or sand when the water sinks, often at a considerable distance from where they fell in.

Some seeds which sink at once in the water can germinate at the bottom and rise to the surface as seedlings, to be drifted away till they are stranded on

a bank, where they can continue to grow. In this way the American Monkey Flower (*Mimulus*), escaped from gardens, is rapidly making its way along the banks of many rivers and streams all over England. It is also thus that the rushes (*Junci*) spread over our damp pastures.

Other seeds may be transported by being blown into the crevices of drifting logs or of floating pumice stone cast out of volcanoes, or in or upon floating masses of ice.

The floating surface plants, *Lemna*, *Azolla*, etc., float entirely on the surface and are thus dispersed, frequently, in cold climates, sinking to the mud beneath and wintering there, and then rising to the surface with the spring rise of temperature.

Whole plants bearing fruits or branches may be carried away by floods or spates, and dispersed over the flooded plains when the water drains away, as tumble-weeds are whirled across dry steppes and plains by the wind.

Marine *Algae* seem to owe nearly all their distribution to the drift of the plant in currents, or by growing on logs or other drift material, rather than to the wide dispersal of their spores.

Vegetative organs, bulbils, winter buds, rhizomes, are frequently water-dispersed also. Some seeds and fruits which are light enough to float belong to inland plants which cannot thrive on river banks, marshes or sea-coasts, so that their buoyancy is useless and quite ineffective. It is an adventitious buoyancy. In most sea- and river-dispersed plants the fruit or seed is specially modified to be able to float a long time without becoming water-logged and sinking. The distance and time that they can float differ very much, but in river plants even a few days enable the plant to migrate for some miles in a strong current.

It is essential that water-dispersed seeds or fruits should belong to plants whose habitat is a wet river bank, pond or marsh, or a sea-coast, whether of tidal mud, sand or shingle, so that not only must the seeds be adapted for water-dispersal, but the plants themselves must also be modified for growth in wet or swampy spots, or more or less saline mud or sea sand.

A good deal has been written by various authors on dispersal of plants by sea and river, but the most important works, especially on sea transport, are those by Guppy in the "Observations of a Naturalist in the Pacific" and "Plants, Seeds and Currents in the West Indian Islands and the Azores," and by Schimper, "Indo-malayische Strandflora," and papers by Hemsley, Praeger, and others.

I treat of the various methods of water-dissemination in the order of the amount of water employed, from the short dissemination by rain-wash to the further rush of mountain streamlets, rivers and floods, which are only continental dispersals, and the migration by sea-currents from one mainland to another and from one island to another, in which frequently the distances of the wanderings of plants are often to be counted in hundreds of miles, their spread being only bounded by the limits of currents.

PART I

DISPERSAL BY RAIN-WASH

Though Kerner seems to consider that the dispersal of seeds by rainfall and rain-wash is comparatively rare and unimportant, this is by no means the case. Rain is of the greatest importance to small seeds which have been shaken from the capsules of the herbaceous plants and fall to the ground, or have been blown away from the tall inflorescences, as in the Foxglove and *Oenothera*. It has a secondary effect in the dispersal of such seeds by carrying the fallen seed further away from the mother-plant, and usually a great deal further than the seed has gone by wind and fall. Many of these herbs would have a very limited area of habitat were it not for the rain-wash which disperses their seeds. Moreover, the rain will run along a road or open space for a considerable distance, carrying the silt and fallen seeds, and, draining away, leave the seeds in a damp rich bed of silt very suitable for their growth. This is easily seen in gardens, where the rain runs down the paths to a drain-pipe and deposits at the mouth of the pipe a quantity of washed-down mud, which, if allowed to remain, soon produces a crop of weeds. It is mainly due to rain that neglected garden paths become covered with moss, grass, and other weeds. It is quite immaterial whether seeds so dispersed can or cannot float. The round polished seeds of the Blue Hyacinth, which possess no buoyancy at all and sink in water at once, are carried along my gravel paths as well as the light grains of *Poa annua*, which are easily blown along by the wind.

In the Botanic Gardens of Singapore was a broad gravel path, about 200 yards long, which came to a level after about 100 yards of gentle slope. On this level a large patch of the little annual weed *Borreria setidens* used constantly to appear. The patch would be several feet across, and the seedlings must have been many hundreds in number. Though the path was often cleaned of them, they appeared again and again after rain. The seeds were washed down from the surrounding hill slopes, where the plant was not very abundant, only occurring as a weed in the cleared spaces surrounding the Palms which grew there, so that the seed must have been actually washed through the mat of grass on the turf slopes before it reached the path. These little Rubiaceous weeds, *Borreria*, *Spermacoce*, *Oldenlandia*, etc., are mainly road-side or open-ground species, and travel along newly-opened roads, through forest or plain, with considerable rapidity. In the first instance, these herbaceous weeds may be blown from the plant to a short distance, or they may be passed by cattle feeding on the plant, or, as often happens in annuals, the whole plant may perish, leaving the seeds or small 1-seeded fruit on the ground. The rain falls and the seeds are washed along till they come to rest on a well-manured spot which is damp enough for them to germinate and reproduce themselves. In addition, the seeds evacuated or regurgitated by birds are very frequently spread to a greater distance, and separated from each other by rain-wash. Birds usually evacuate while sitting on the branch of a tree or on a railing, or the back of a seat and similar spots, and the seeds passed in the evacuation are sooner or later washed away by the rain to a more suitable spot for growth.

The parasitic mistletoes have a viscid slime in the berries which attaches them to the tree-branch, and so prevents this. I have often seen the droppings of birds containing seeds of *Ilex*, *Pyracantha*, etc., washed off the bough or railing on which they were deposited, and so dispersed. The same thing applies to seeds regurgitated on the ground. Blackbirds used to eat the berries of a *Pyracantha* in my garden, and regurgitate the seeds in a mass in the road. The first rains that came afterwards washed them far away.

In fact, all small seeds, and in the tropical rain-forest large and comparatively heavy seeds, are rolled along to a considerable distance by the violent rainstorms. On Gunong Pantai, in Johor, on one occasion the stream by which it was the custom to camp had disappeared, and I found only the bed marking its position. It was quite dry. In half an hour rain began to fall, and in less than an hour the stream was again full, and so it remained during the ten days I was in the forest. Temporary rain-wash streams like this carry a large number of fallen fruits and seeds along from the higher ground. Many of the tropical forest trees possess heavy fruits and seeds which have no way of dispersal except by rolling along after they have fallen, and later by being swept further along by heavy torrents of rain. Floating seeds like those of *Bassia* (*Sapotaceae*) are swept by such torrents into streams, and continue to float away till the fall of the water, when they are stranded and able to grow.

In fact, it may be said that the rain-wash collects the seeds from all over the forest and carries them down to any spot where they can lodge, or into streams. It is only by rain-wash that the small-seeded herbs of the tropical forests, *Sonerila*, *Begonia*, *Argostemma*, *Ophiorrhiza*, can be carried from one place to another.

Perhaps the most interesting of the Malayan jungle herbs are the *Gesneraceae*, *Didymocarpus*, *Loxocarpus*, and other small-seeded capsular genera. These herbs frequent the rocks and banks in dark wet forest. They possess long, narrow cylindric capsules, broad at the base and narrowing towards the tip. They dehisce along the upper line, forming a kind of gutter narrowed to the tip, which points somewhat downwards.

The *Loxocarpi* have shorter, wider capsules than *Didymocarpi*, nearly ovate; when dehiscing, the seeds are slowly washed out, in the same way as in *Didymocarpus*, and grow on the surface of dripping mossy rocks in the forests.

Boea, a genus allied to *Didymocarpus*, inhabits limestone rocks where there is a dry season, or, if they persist on limestone cliffs in the wet rain-forest region, retain their habit of completely drying up themselves at a certain period (as they do in some of the limestone cliffs of the interior of the Malay Peninsula). They differ from *Didymocarpus* and *Paraboea* in having the long slender capsules spirally twisted in dehiscence, like the pods of many Leguminous plants. They fruit in the dry season when there is no rain, and I believe that the seeds are ejected from the capsules by the spiral dehiscence, as in the *Leguminosae*. A similar type of capsule is found in *Streptocarpus*. It is clear that the *Boea*, fruiting in the rainless period, would not have the advantage of the *Didymocarpi*, in the ever-wet forests, of dispersal by rain, and if the spiral twisting did not exist to expel the seeds from the capsule, they would not be dispersed at all. The seeds are minute, innumerable, and papillose or ridged. In *Didymocarpus*, when the capsule dehisces, the raindrops, falling on the wider base, run down to the point, carrying with them the seeds, which are pushed down to the tip of the open gutter, and fall, a few at a time, in the raindrops upon the face of the rocks or the bank below.

The seeds are papillose or ridged, never smooth, so that they may catch on the surface of the rock or ground, and not be carried far away. Were they smooth they might be borne down into the forest streams and eventually into the rivers, and so be lost.

This papillation, striation, or scrobiculation of the seeds is very common in plants which grow in such situations, as well as in plants which grow in shallow waters. Beautiful examples of these anchoring processes are seen in *Philydrum lanuginosum* (*Philydraceae*), which has vase-shaped seeds, narrowed at both blunt ends, and covered with short prominent cylindric papillae (Pl. XII, fig. 16). It is a tall narrow-leaved plant growing in shallow water only a few inches deep. The Aroid *Cyrtosperma lasioides*, also a shallow-water plant, has flat seeds with a crested papillose ridge.

The section *Gardeniella* of *Gardenia* (*Rubiaceae*) are plants with the habit of *Didymocarpus*, dwarf, with a shrubby base and long narrow capsules of minute seeds. They are found on banks in the dense forests of the Malay Peninsula, and have much the same dispersal methods as the *Didymocarps*. The section is connected by *G. tentaculata*, in which the fewer but much larger seeds are distributed by rivers, on the banks of which it grows with the typical tree *Gardenia*, which has fruits dispersed by mammals and birds.

It is probable that most of our common roadside plants owe their abundance to the rush of rain in the winter, many species having no other very definite or reliable means of dispersal.

Although rain-wash in the plains, both of temperate and tropical regions, is of very great importance in the dispersal of seeds, its action is accentuated in the mountain forests of the tropical rain zone. Frequently from the mountains in the interior of the Malay Peninsula, during a rainy period, immense masses of the hillsides break away and slide down to the valleys, carrying with them trees and bushes and innumerable fallen seeds and fruits. One of the dangers of camping on these hill slopes is that at night a mass of hillside may slide down suddenly and cover the camp with tons of earth and rock. A fall 7 miles long was reported in the Semangko Pass some 15 years ago, the hills here being about 4,000 feet high. The denudation of these mountains is gradual but continuous, and many of the seeds and fruits brought down by these falls must drop into the stream at the base of the valley and be carried on to the plains at the foot of the hill. The rain-wash which brings down the silt to form the ever-increasing plains between the mountains and the sea brings down also the seeds which form the jungle which will eventually cover the newly-formed ground with a dense vegetation.

Periodically the rush of water from the mountains, especially in tropical regions, is enormous, resulting in great floods and a large deposit of silt which gradually pushes the land out into the sea. In the floods of 1926, in the Malay Peninsula, some of the rivers rose from 60 to 85 feet above the normal height, and silt brought down from the mountains lay from 5 to 6 feet deep on the ground in the low country. In such rushes of water vast numbers of seeds must be brought down from the mountains and strewn in suitable positions for growing in the plains below.

It is in this way that plants are very widely and, geologically speaking, rapidly diffused over continents and large islands. It is not necessary for the seeds so dispersed to be able to float. A rain-wash which can carry sand and stones for a long distance can carry any kind of seeds with it, and as the water runs off and the flooded land becomes dry, a large proportion of the seeds will grow and establish themselves, and there can be little doubt that many widely distributed plants, the seeds of which have no special modification for dispersal by other means, owe their extensive distribution to this form of dissemination.

In the case of many large or moderate-sized fruits in India, and probably all over the tropics, the pulp or shell of the fruit dries up and cracks, or is eaten by white ants (*termites*), which usually pile up fine earth over the fruit. The seeds, unhurt by these insects, are then washed away by the heavy rains

and dispersed with the soil. This takes place in *Dillenia indica* (*see under* River Dispersal, p. 198), and in *Schleichera trijuga*, which have tolerably heavy seeds, from 40 to 50 to the ounce, and *Acacia Farnesiana*, from 200 to 300 to the ounce, according to Troup.

The importance of rain-wash in diffusion of seeds, especially of herbaceous plants, both in open country and in forest, is thus seen to be very great, and by no means a negligible method of dissemination, as suggested by Kerner and others.

I give the following notes on rain-dispersed plants :—

Illecebrum verticillatum (*Illecebraceae*).—This forms round flat turfs of prostrate rooting stems from 6 to 12 inches long, covered with small leaves. The fruit is subsessile, in fascicles of 3 or 4 in the axils, small, ovoid, membranous, opening in 5 or 10 valves, 1-seeded. This plant grows at Kingsmere, in Berkshire, where I have seen it on sandy heaths. It evidently spreads along the paths, and is most abundant below the slopes, as if it had been washed down. The branches, in plants in Kew Gardens, dry and break off during the winter, and are carried along by rain-wash. The plant does not grow in or near water, and wind can play but little part in dispersal. At least locally it is clearly spread by the dispersal of branches and seeds by rain-wash.

Striga lutea (*Scrophulariaceae*).—This little parasite plant is said by Mr. A. M. Sawyer to be dispersed by moving water, i.e., rain-wash.

Matricaria discoidea.—This plant, though carried about on the feet of man and animals to distant spots, then continues its migration largely by rain-wash. The whole plant generally dies and disappears in England in winter, and the achenes are washed along by the rains. I have seen it distributed thus on Holmwood Common, Surrey. The plant had been conveyed by human agency along the paths, and the achenes later had been washed down the drainage runnels leading from the paths, and was growing there abundantly.

Very many of the grasses owe their rapid dispersal to rain-wash. *Poa annua* is not only dispersed by wind, its grains remaining enclosed in the glumes which act as wings, but they are carried by rain-wash as well along paths and roadsides, and even streets, as can be seen anywhere in England. Other grasses thus dispersed are *Holcus mollis*, *Hordeum murinum*, *Avena sativa*, and in the tropics, *Eleusine indica*, *Digitaria chinensis*, *Eragrostis unioloides* and *E. tenella*.

Other small plants I have seen which have been clearly spread along paths and bare ground by rain-wash are *Cardamine hirsuta*, *Senebiera coronopus*, *Claytonia perfoliata*, *Arenaria serpyllifolia*, *Sagina apetala*, *Anthriscus sylvestris*, *Lotus corniculatus*, *Bellis perennis*, *Ambrosia artemisiaefolia*, *Centipeda orbicularis*, *Lapsana communis*, *Borreria setidens*, *Oldenlandia corymbosa*, *Solanum nigrum*, *Erythraea capitata*, *Asperula cynanchica*, *Prunella vulgaris*, *Polygonum aviculare*, *Scilla nutans*, *Eriocaulon truncatum*.

Cedrela Toona (*Meliaceae*).—In India, Troup states that the winged seeds, which are ½ inch or more long, are dispersed by rain-wash as well as by wind. " Toon saplings are often found in hedges and bushes where they have been " washed by rain, so that they get protection from sun."

Terminalia tomentosa.—Troup gives an interesting and instructive note on the dispersal of the fruits of this tree. The fruits are rather light, about 1 inch long, with 5 low wings, oblong in outline. They are dispersed by wind to some extent and also by rain-wash. He writes :—" A good instance of the " value of loose soil was observed a few years ago in the Gonda district of " the United Provinces (of India), when vigorous seedlings suddenly appeared " in large numbers on loose earth washed down along the base of the ridge " of earth thrown up along a new boundary trench. The abundance of these " seedlings was due to the fruits having been washed against the base of

"the ridge and partly covered by the soil, and indicates that surface water "in the rains is an important distributing agency."

D. Griffiths (in "A Novel Seed Planter," *Torrey Bot. Club Gaz.*, 1902, p. 164) gives an interesting account of the planting of the seeds of *Plantago fastigiata* (*Plantagineae*), known as Indian Wheat, in the Arizona deserts. The plant seeds heavily in March, and yields 1 ton of air-dried seed per acre. In April the seed was quite ripe, and in May was scattered all over the Meza. The seeds, as is usual with Plantains, are covered with mucilage, which, however, is more pronounced in this and other dry land species than in the ones which grow in dampèr spots, and the whole seed, when wet, is enclosed in a jelly. Numerous seeds collected in depressions, at first forming a mass of seeds, mucilage and debris. After a time the seed separated largely from the refuse, and a crust was produced above and below, the upper layer formed by rapid evaporation, the lower by mixing the drier earth below it with mucilage, the dry earth abstracting the moisture. These cakes of seed, mucilage and debris were often found 2 feet wide and 3 inches thick. Seeds in these masses probably perished. In the case of seeds which were not washed together, every seed was sunk in a little pit, the walls and bottom of which became rigid by the hardened mucilage. The seed was not then covered, but silt and sand would eventually cover it and leave it in a very satisfactory position for germination. The function of the mucilage is to bury the seed, which is effected by the contraction, by loss of water, of the expanded mucilage, which is firmly attached by the outer and lower edges to the particles of soil, resulting in the compacting of the silt below the seed and the coat, so as to form a pit.

Many of the lower *Cryptogams* owe much of their dispersal to rain-wash. *Marchantia polymorpha*, a very widely distributed Liverwort, is much dispersed in this way. On the flat thallus, cups are produced containing thallidia or gemmae, and the papillae at the base of the cup form a gelatinous mass, which swells up and raises the gemmae up to the edge of the cup, when they are washed out by rain-water. Similar examples are those of the gemmae of the crescent-shaped pockets of *Lunularia*, and the flask-shaped cavities of *Blasia pusilla*. In the mosses also these thallidia are frequently produced on the surface of leaves, in *Leucobryum*, *Grimmia*, *Zygodon*, *Orthotrichum*, *Barbula*, and many other species, and these are washed away by rain-water to form new plants.

Yeates (in "The Means of Distribution of *Hepaticae*") is strongly of opinion that most of these plants are dispersed by water. In Britain, at least, the production of spores dispersed by wind is very rare in such plants as *Marchantia polymorpha*, *Lunularia cruciata*, *Fegatella conica* and *Pellea epiphylla*, which mainly spread by water-carriage of gemmae, spores or detached plants during floods.

The Covering of New-Formed Land.

In large areas, whether continental or big islands, where denudation is extensive and continuous, the silt derived from the interior mountains or hills depends on the constituents of the inland soils. With the silt is washed down a large number of seeds of the plants of the hinterland, which form the vegetation of the ground. In fact, it may be said that the plants move on with the silt. But this mountain or inland flora is checked when it gets near enough to the sea, and is prevented from establishing itself by the action of the salt. Hence we get a coast flora fringing the land which consists of plants adapted to life under saline conditions, the littoral flora, which is derived from other similar coasts by sea-dispersal. As more and more inland silt comes down, the sea-edge is pushed out further and further, and the littoral plants are either

exterminated by the advancing inland vegetation, or are modified to adapt themselves to the changed conditions.

Occasionally a few persist, surrounded by an inland flora, long after the sea has receded many miles from them. Thus I have found *Pisonia excelsa* by the limestone rocks in forest now about 36 miles from the sea; *Boerhaavia repanda* on Chupeng rock in Perlis, now some miles from the shore; and *Cycas Rumphii*, a regular seashore plant, far away from the sea in dense forests in the interior of the Peninsula. These isolated relics of a vanished littoral flora did not appear to spread. They merely held their own place, only a few specimens remaining, except in the case of the *Cycas*, which seemed to have long ceased to flower, and reproduced itself merely by bulbils. Guppy mentions a number of littoral plants remaining mixed with inland plants on the rolling plains at the foot of the mountains in Vanua Levu (Fiji Islands), *Cerbera*, *Morinda citrifolia*, *Casuarina*, *Cycas*, and *Ipomoea pes-caprae*, evidently the remains of a sea-coast flora holding its own against the encroachment of an inland one. The *Cochlearia officinalis*, which grows at the foot of Cheddar rocks, now far from the sea, is another littoral plant growing inland, and the littoral mountain plants found in the Scotch and Welsh mountains may also be accounted for in this way.

PART II

DISPERSAL BY ICE, STREAM, RIVER AND FLOOD

Foreword—Ice and Iceberg Transport—Vegetative Portions Dispersed by River and Flood, Floating Stems—Submerged Plants Dispersed by Detached Portions, Buoyancy of Branches, Submerged Rhizomes, Bulbils, Winter Buds—Movement of Plants in Mass down Rivers—Floating Seedlings—Heavy Seeds Drifted under Water—Wash-out of Buried Seeds—Floating Seeds and Fruits—List of Seeds and Fruits Dispersed by River.

FOREWORD.

ANYONE walking by the side of a river in the autumn will be struck by the abundance of fruits, seeds and fragments still alive of aquatic or river-bank plants thrown up on the banks with other river debris. Among them frequently are to be found a number of seeds and fruits in good condition. These seeds and fruits are those that possess modifications for floating unharmed, and are usually plants which inhabit river banks or low-lying fields which are flooded by the rise of the river. Most of the plants which inhabit dry inland spots have non-buoyant seeds, or, if they do float for some time, they are soon decayed by the action of the water. But most of the river-bank and aquatic plants have buoyant seeds. Of these, some float for a day or two only, some for a week or more, and some for months. Some marsh or stream-bank plants have seeds which sink at once, germinate under water, and float as seedlings (*Juncus*, *Mimulus*). (These are treated in a section on p. 187.) Even seeds which float only a day or two can travel very considerable distances in that time in a rapid-flowing river. Eventually the floating seeds are drifted to the shore and stranded by the fall of the water, or sink at the shallow places, where they may grow.

It is not a very great advantage for the seeds of river plants to have a long period of buoyancy, as it is in the case of sea-dispersed seeds, for they might be carried into water too brackish for them, or into the sea and be lost.

In tidal rivers seeds and fruits may migrate from the mouth of the river upwards, which is a common thing for them to do. *Scirpus maritimus*, for instance, is slowly moving up stream in the Thames above Kew Bridge.

Seeds may be transported from one river to another by floods, or by a change of the direction of streams and rains. It is clearly essential that plants which grow in deep water must have seeds which are heavy and which sink sooner or later, and at the same time must have some means or system of dispersal from one body of water to another. If when ripe they sink to the bottom and remain there, they cannot spread unless the water at the bottom is moving so as to carry them along. This may happen in rivers, especially rapid streams, but it cannot do so in lakes and pools. There are several systems by which water plants can move about. In some cases the fruit comes to the surface before dehiscence, and the seeds float for a short time in a mucilaginous mass formed by the placentas or part of the pericarp, and either drift along the surface by current or wind, or become attached to water-fowl, or may be swallowed by them and so borne away. Such are the Water-lilies *Nymphea* and *Ottelia*, and *Limnanthemum*. In some the seeds float at first, having aeriferous tissue in testa, or perisperm or chalaza. These portions of the seed eventually decay and the seed sinks. This allows of their floating long enough before

sinking to be transported to a distance by currents and also by birds. A considerable number of aquatics are dispersed by fragments of the plant, or whole plants, such as *Lemna* and *Azolla*, which are drifted away or become attached to birds and are borne away by them.

Of the fruits and seeds brought down the rivers from inland to the sea, a great many perish in the water. This appears sometimes to be due to their beginning to germinate too soon, long before they are stranded so that they can continue their development, and they therefore die. In other cases of riparian plants, they appear to be destroyed by the action of sea-water or to become water-logged by prolonged immersion.

I have seen the fruits of *Dipterocarpus obtusifolius*, a fruit frequently dispersed successfully along the river banks by a comparatively short immersion, floating at sea off the east coast of the Malay Peninsula, all dead and mostly decayed.

On the shores of the Malay Islands no seed is more abundant in sea-drift than that of *Pangium edule*, a river-bank tree, with large oblong fruits which contain a number of woody seeds, ovoid and angled, about 2 inches long, yet this tree is apparently confined to the Malay Peninsula and Java. The husk of the seed, when picked up on the shores of Cocos and Christmas Islands, is usually empty. The seeds are very oily, and oily seeds, it may be noticed, have a short life-duration. *Hodgsonia capniocarpa*, a cucurbitaceous plant, is also a river-side plant of which the seeds are carried out to sea and destroyed in like manner.

Many seeds which are too heavy of themselves to float are assisted by being attached to the light capsule or a part of it, or, in the case of grasses, to the glumes, and can drift like this a long way. On the banks of the Tay, in Perthshire, the shrub *Lupinus nutkaensis* (a garden escape) is very abundant in gravelly beaches, and clearly spreads by water. The seeds themselves sink at once when they fall into the water, but a valve of the pod to which one or two seeds are attached will readily float. I have no doubt it is mainly in this way that the plant is spreading along the banks of the river, but even the seeds which fall into the gravelly stream-bed may be washed along the bottom and be thrown up by the rush of water, unhurt on a forming beach, with the heavier sand and pebbles, and so establish the plant.

The achenes of *Ranunculus flammula* sink at once in water, yet the plants are found fringing the shallow streams on heaths and similar places in such a way that it seems impossible to avoid the inference that the achenes have been spread by water. This is probably effected by winter rains washing them up with sand from the bottom of the streamlet, and I think many of these common marsh plants are dispersed in this way.

The amount of seeds drifted in a river is shown to be enormous by W. L. McAtee (*Ecology*, 1925, vi, 288). He examined the drift in American rivers, and gives a long list of seeds and insects which he found floating there. Most of the species he records are buoyant seeds and fruits, but many, like *Scirpus Americanus* and grasses, are not adapted for floating. He gives a list of 2,490 seeds taken from a patch of drift 6 inches square, including many of these non-buoyant seeds, of sedges and grasses, and also tubers of *Cyperus*. He quotes G. E. Egginton and W. W. Robbin, who calculated the number of seeds carried along in irrigation ditches 12 feet wide, with a current velocity of 1 foot per second. They found that from 4,000,000 to nearly 9,000,000 were drifted along in 24 hours. A large number of small fruits and seeds are transported, floating on debris, fragments of sticks, leaves, etc., and he gives a list of 166 seeds found in the grooves of a drift shell of a black walnut. These included the following:—*Naias*, *Panicum*, *Echinochloa crus-galli*, *Setaria* (2 species), *Homalocenchrus* (2 species), *Muhlen-*

bergia, Eleusine indica, Cyperus, Alnus, Boehmeria, Rumex acetosella, Persicaria, Chenopodium, Amaranthus, Portulaca oleracea, Mollugo verticillata, Alsine, Lepidium, Rubus, Oxalis, Acalypha, Chamaesyce, Sambucus, Ambrosia, Eclipta alba.

This account shows clearly that vast numbers of non-buoyant seeds may be transported on debris in a flood as well as those which are buoyant, though obviously the actual dissemination may not be quite as satisfactory as in the case of a buoyant seed.

Mountain Streams and glacier streamlets may carry seeds or plants from the highest parts of the mountains to the plains, especially during the rush of the autumn rains and after the melting of the snows. Many of these seeds and plants must fail to establish themselves in the lowlands owing to the difference in the climate and environment, but some appear to adapt themselves to the change of circumstances and make a satisfactory lodgment on the silt or on the river bank. I have, however, few records of this method of dispersal. In India, in 1912, Mr. Davies, of the Lucknow Botanic Gardens, told me he frequently found, growing on the banks of the river at Lucknow, strange mountain plants brought down by the river from the mountains far to the north.

Massart (in "La Dissemination des Plantes Alpines") records the occurrence of *Saxifraga aizoides* and *Trifolium saxatile* in the Alps in alluvial flats in cultivated ground brought down by the glacial streamlets, and on the mouth of the Gorner glacier and near the source of the Rhone he found *Pinguicula vulgaris, Linaria alpina, Trifolium alpinum* and *Senecio incanus, Silene exscapa*, and *Primula farinosa*, all high alpine plants, which had been brought down by the glacier streams.

Trifolium saxatile has the small pod enclosed in a plumose calyx, and this is probably first blown on to the glacier and, falling into the stream, is carried far away down the slopes.

Saxifraga aizoides has minute seeds in a capsule. I have no record as to whether they will float or not (though, as Guppy records those of other *Saxifragas* as being non-buoyant, they are probably similar), but anybody who has been in the Scotch mountains must have noticed the stream edges fringed with these pretty yellow-flowered plants, and there can be no doubt that the seeds are dispersed by the rush of water along the rocky edges of the burns.

In 1921 I found the high alpine *Veronica humifusa* on the banks of Loch Lomond, where either its seeds or perhaps the whole plant had been washed down by the streams from the mountain-side, and on the Tay banks (Perth), near Stanley I found *Rumex alpinus* (a plant drifted down from gardens) growing upon the shingle beaches, and *Alchemilla alpina*, brought down from the far-distant mountains. In these cases I believe the whole plant was washed down and, drifting up at the river side, became established there.

The amount of fruits and seeds carried down by big rivers, both of temperate and especially of tropical regions, is enormous, and many travellers record the vast quantity of timber, branches of trees, fruits, seeds, and other vegetable detritus which can be seen drifting out to sea from the estuaries of these big rivers. Thus Moseley writes ("Notes of a Naturalist," p. 367) :—

> "As we neared Dobbo (Aru Islands), turning up the passages between the "two islands, we passed large quantities of leaves, fruits and flowers and "branches of trees floated off from the shores, and now drifting about mingled "with a floating seaweed (*Sargassum*). . . . I was astonished at the large "quantities of fresh vegetable matter thus seen floating on the sea. Not only "are large quantities of fruits capable of germinating, thus transported from "island to island and transplanted by the waves, but entire living plants, "even trees, are washed from island to island and transplanted by the waves."

He also describes (p. 432) the drift from the Ambernoh River, in New Guinea. "So large is this river that even at this great distance (70 miles from the Point "Durville, where it runs into the sea) we found the sea blocked with the drift-"wood brought down by it. We passed through long lines of driftwood "dispersed in curves at right-angles to the direction in which lay the river's "mouth. Among the logs were many whole-rooted trees."

He also mentions the stems of a large cane grass (probably *Saccharum*). One of these cane stems was 14 feet in length and from 1½ to 2 inches in diameter. Among the floating timbers were the usual littoral seeds—those of 2 species of *Pandanus*, and of the Puzzle seed, *Heritiera littoralis*, fruits of *Barringtonia* and of *Ipomoea pes-caprae*. But besides these fruits of littoral plants there were seeds of from 40 to 50 species of more inland plants. Very small seeds were as abundant as large ones, the surface scum being so full of them that they could be scooped up in quantities with a fine net.

Guppy gives a good deal of information in the drift off Hawaii, Ecuador and Fiji. He notes the occurrence, on the shores of Hawaii, of horse and goat dung as common and not broken up, and that sometimes seeds are to be seen in the stranded material. This material is not likely to travel very far before being broken up, but seeds of grasses and small herbs might be carried by this means to some distant spots. It is more likely, however, that seeds of the smaller herbs might be carried in the soil attached to roots of trees, etc. (such as the clump of sugar-cane which drifted at least 700 miles to Cocos Island), or in the interstices in timber and pumice. It is, however, noticeable that comparatively few of the inland herbaceous plants appear in oceanic islands before the settlement there of man. Still, there are grasses, especially such plants as *Panicum* and *Paspalum*, in islands like Christmas Island, whose presence is very difficult to account for unless they were borne there in some such way. There is no doubt that terrestrial molluscs, ants and other insects, and earthworms, do reach remote islets unaided by man, and it is difficult to see how they can reach these shores unless they travel on or in floating driftwood, or in the interstices between the roots. The means of transport of these animals from island to island seems to have been very little studied, so far as I can find, but if they can be carried in some such way across the seas, the minute seed of grasses or other herbs might easily be transported in like manner.

F. Wood Jones reports finding a big tree drifted to Cocos-Keeling Island with a barrow-load of red earth in its roots, and suggests that the little earth-snake *Typhlops braminus*, now found on the atoll, might have come in some such way. However, we several times sent cart-loads of soil from the Botanic Gardens, Singapore, to Cocos Island, and as this little animal was quite common in the Gardens, it may have been introduced in that way.

Floods.—Though floods are not usually regular in their appearance, they are so common in many areas that they play a very important part in the dispersal of many plants. They are mainly due to big rivers passing through a large flat plain and deriving their water-supply from a mass of mountains or a large well-watered tract. These flood plains are usually formed of silt brought down from the mountains, either existing at the present day or formerly, and now so denuded as to form the flood plain. Such flood plains are those formed by the Rhine, Nile, Kistna and other Indian rivers, the Mississippi and Missouri.

At intervals these rivers overflow and spread over the flat lands for many miles, often from 50 or 60 miles, sweeping with them seeds and floating aquatic plants, as well as other vegetable debris. The flood plain of the Mississippi is stated to be from 20 to 80 miles wide, and occupies 50,000 square miles. Floods from the Kistna, in India, are known to have been from

40 to 50 miles in length. These floods form lakes, streams and pools, and overflow into other river areas, carrying with them seeds of riparian and various aquatic plants.

There are a number of aquatics which do not grow in running water, but only where it is stagnant, such as *Azolla*, *Lemna*, *Pistia*, *Trapa*, *Hydrocharis*, *Hottonia*, etc. The dispersal of this class is mainly due to floods, though some are further dispersed by adherence of seed or the whole or portions of the plants to birds. But many seem to have arrived in the isolated pools and lakes where we find them, simply by transport in floods. The tendency of some of these aquatics to become scarce and disappear in countries where civilisation has caused the restriction of rivers to definite beds and certain routes, and the means taken to check the spread of floods, may be due to such causes. *Trapa natans*, formerly apparently common in England and on the Continent, is restricted now to a few isolated areas in France, Spain, Germany, Switzerland, Italy, the Balkans, and Russia, and has quite disappeared from England, Holland, and a few other countries. *Brasenia peltata*, formerly occurring in Russia, Denmark, Germany and Switzerland, has quite disappeared from Europe. *Stratiotes*, formerly a genus of several species, is now reduced to one very local one in England, and several others of these stagnant-water aquatics were clearly more widely distributed in prehistoric times than they are now.

Many of the older lakes and marshy spots in England have been reclaimed by man, and with their disappearance we have lost large areas of water where these plants formerly grew, and which were transported across the country by floods and rushes of water. Such disappeared habitats are the fens of Cambridge, the lake at Glastonbury, Port Meadow Lake at Oxford (deep enough for the hippopotamus in Pleistocene times), the large marsh and water-area at Southport. All these suitable habitats for the floating aquatics have disappeared, and these plants have become very much localised.

Ice and Iceberg Transport.

The transport of seeds by ice has naturally occurred mainly in the Arctic and Antarctic areas of the world. Seeds may be conveyed from place to place by both icebergs and shore-ice drifting from one shore to another.

Lyell ("Principles of Geology," chap. xv) deals with transportation of solid matter by ice, chiefly as dealing with the conveyance of boulders and pebbles in surface and ground-ice. Pebbles and small pieces of rock may be seen carried down the river entangled in ice, and he considers that the principal transfer of pebbles and stones adhering to ice goes on under water, unseen. It is obvious that ice which can pick up and transport pebbles and stones from the bottom of a shallow stream, or a shore edge, may easily transport seeds which have sunk in the water or drifted upon the shores. The importance of this method of conveyance seems to lie in the fact that seeds which cannot float may be dispersed in this way. He states that masses of ice formed at the bottom of rivers (in the Thames, and Siberian rivers), drift up to the top and convey stones, etc., lying on the river bed. This may account to some extent for the dispersal of riparian plants which have no other means of dissemination. I have seen holly seeds floating on ice, on to which they had fallen as bird droppings.

Darwin (in "Origin of Species," chap xii) calls attention to transport of soil, etc., by icebergs drifting southwards from the Arctic regions, and especially in the Glacial period. They are known, he says, to be sometimes loaded with earth and stones, brushwood, etc., and even the nest of a land-bird is recorded to have been carried by one. In the Azores, from the large number of plants common to these islands and Europe, compared with those

in more distant Atlantic islands, he suspected that they had been partly stocked with plants from ice-borne seeds during the Glacial epoch. Lyell wrote to Mr. Harting to inquire whether erratic boulders occurred in these islands, and he replied that he found large fragments of granite and other rocks not occurring *in situ* in the Azores. These must have been transported by ice, and Darwin conjectured that if ice carried stones from other countries to the Azores, it might have carried seeds also. Certainly many of the small-seeded *Junci* and *Cyperaceae*, etc., may have been so introduced. Drifting ice may also be responsible for the transport of many plants the seeds of which do not float, nor are carried by birds, throughout the Arctic circle, such widely dispersed plants as *Ranunculi*, Poppies and Saxifrages, and thus may account for their presence in Iceland, the Faroes, Newfoundland, and such spots. Sernander records seeing acorns floating in ice in Scandinavian rivers.

In " The Flora of Greenland and its Origin " (*Det. Konigl. Dansk Videnskab Selskab. Biol. Meddel.*, 1926, vi, 3), C. H. Österfeldt writes :—

" When the sea-ice lies firm through the winter it forms a splendid field " for the transport of wind-borne seeds and fragments of plants. Moreover, " the wind is at that season very strong. When sea-ice is carried by currents, " as is particularly the case in East Greenland, it will also doubtless be able " to carry portions of plants from other countries. This would explain the " occurrence of the peculiar species, e.g., *Polemonium boreale*, *Arenaria pseudo-* " *frigida*, which are positively restricted to the extreme coastal districts, which " seems to argue in favour of this mode of immigration. Even in temperate " regions the ice in winter may play some part in dispersal."

D. S. Johnson and H. H. York, in a paper on " Relation of Plants to Tide Levels " (Carnegie Institute, 1913), give a note as to the dispersal of the grass *Spartina glabra* by ice. They write :—

" Another method of spreading to the more distant parts of the harbour " is through transportation of whole tufts or mats by ice. The stubble may " be frozen in blocks of ice at low tide, and when these blocks float up with " the rising tide, whole clumps of *Spartina* may be lifted and carried to different " parts of the harbour."

In Disko Island (Greenland) M. P. Porsild states that in bad summers *Potamogetons* only reproduce themselves by winter buds, and he also states that the *Callitriche verna*, *C. hamulata*, and *C. autumnalis*, hibernate enclosed in ice. So that broken ice containing pieces or winter bulbs of these plants can be drifted away from one place to another.

In the Antarctic regions ice may have acted in the same way in transporting seeds and portions of plants in drift ice or on icebergs. The flora of the Antarctic regions is, however, very much poorer than that of the Arctic regions. The Marion Isles, however, possess cliffs and shore-ice, and Darwin suggests that Kerguelen may have received its flora by ice drift. The rocks are glaciated, and there are signs of a former large extension of ice in this region. On it are found *Ranunculi*, *Colobanthus*, *Lyallia*, *Tillaea*, *Galium*, *Azorella*, *Juncus*, and several grasses. Most are small-seeded plants, and their seeds might have been carried on the feet of wandering birds, but this, I think, could hardly apply to the *Ranunculi*.

VEGETATIVE PORTIONS DISPERSED BY RIVER AND FLOOD.

Many plants owe their abundance to the dispersal of their vegetative organs, either in detached portions, branches, bulbils, winter buds, rhizomes, etc., or from the floating away of the whole plant. In many cases the plants so

dispersed are aquatic, either surface-floaters or submerged plants, though many riparian terrestrial ones are also so dispersed. Branches of trees and shrubs carrying seeds may be torn off by streams or floods, and carry the seeds to some distance. In some cases floods may disperse plants of quite dry habitats in this way, even such xerophytic plants as *Cacti* and *Salsola Kali*.

The same methods of dispersal occur not only in fresh water, but in the sea. These are treated separately on p. 253.

Very many aquatic and marsh plants inhabit stagnant water, ditches, lakes and pools, and are not found in running water, yet they are widely scattered, often over a very large area. In most of these the seeds sink in water, and except for birds and animals conveying them on their feet, they have no means of dispersal except by floods. Floods, though in many areas irregular and not extensive, in open countries like Africa and India are almost annual, and of very wide extent, and it is to this that many of these plants owe their wide distribution.

Floating Stems.

Some aquatic plants which float on the surface of the water possess enlarged floating stems of a pithy nature, of which portions are from time to time broken off and float away. Such plants are *Neptunia oleracea* and *Aeschynomene asperata* (*Leguminosae*) and *Jussiaea repens* (*Onagraceae*).

In *Neptunia oleracea* (*N. prostrata*) the swollen joints, which are cased in a thick felt of white fibres, are about 3 inches long and 1 inch thick. They are easily broken off, and each portion grows readily. The plant is found floating in rivers or pools in Africa, Madagascar, India and Brazil. It is popular with the natives as a vegetable, and is often cultivated. In the Malay Peninsula it is found usually in ditches, where it has escaped from cultivation.

Aeschynomene asperata has also pithy floating stems, and is a native of India, where it plays a part in the making of the Sudd, under which heading an account of it is given. (*See* p. 185.)

Jussiaea repens (*Onagraceae*) is a widely distributed floater usually found in ditches and ponds all over the tropics. It has a rather more slender floating stem, any bit of which will grow.

Trapa natans (*Onagraceae*) (the Water Chestnut).—A floating plant apparently common in Europe, including England, in Pleistocene times, but now largely disappeared. There are several allied species, *T. bispinosa*, etc., and both these and *T. natans* are found in ponds and lakes in Europe, and in Africa: The plant is dispersed both by rosettes on long stolons and by its curious bull's-head-shaped fruits. The petioles have a dilatation in the centre, reminding one of those of *Eichornia*. It is recorded as floating in the stream of the Nile and other rivers. Kirk (in Kew Herbarium) writes:—" This comes " down in large quantities when the Shire (Zanzibar) is in flood." Grant (in " Speke's and Grant's Travels ") says the shores of the Victoria Nyanza are strewn with its fruits.

In some places it is cultivated for its fruit, but chiefly owes its dispersal to the floating powers of the plant and its seeds.

Phyllanthus fluitans (*Euphorbiaceae*) is a very odd little species of this large genus of terrestrial shrubs and herbs, which has the habit of a *Salvinia*, a free floater with rounded leaves. It inhabits the Brazilian rivers, and is apparently very rare, as it has only once been collected (by Spruce). It has small capsular fruits like an ordinary *Phyllanthus*, the seeds of all species of which genus, so far as is known, sink in water.

The beautiful Water Hyacinth, *Eichornia crassipes*, inhabits the water

meadows of Pernambuco and other parts of Brazil. It produces stolons bearing tufts of leaves with dilated petioles, by which it can be floated on the surface of the water. In the flood times the plants in the water meadows are torn up, and the stolons being broken, the young plants drift away over the country and down the rivers. On account of the beauty of its flowers it was introduced into the Old World about 1829. In Asia and Australia it appears to reproduce itself only by the vegetative process, and does not produce seed, but it grows to such an enormous mass and so rapidly that it has choked up many rivers in Australia, Florida, and Cambodia in a very short time, and proved a serious obstacle to water traffic. It was introduced into Java about 1886, and from there was brought over to Singapore, where the Chinese cultivated it at first for its ornamental flowers, which they sold in bunches in the streets. Later they adopted it as a pig food. It did not thrive as an escape in Singapore as it had done in Australia and other places. I found it would only grow in shaded ponds, our rivers being too brackish, for, like *Lemna*, *Azolla* and *Pistia*, it soon perished where there was even a little salt in the water, and it evidently would not thrive in the full sun of the Equator.

Somewhat similar to the history of the spread of *Eichornia* by stolon-buds through floods is that of many other aquatics which produce winter buds or stolon-buds, such as *Stratiotes*, of which the shoots and buds break off in winter and drift away; *Vallisneria*, of which stolon-buds become detached in winter; *Utricularia*, *Hydrocharis*, *Hottonia*, *Callitriche* and sometimes Potamogetons, are dispersed in this way.

In *Hydrocharis* the winter buds appear to sink at once to the bottom when detached. Still, undercurrents or violent rushes of flood water may distribute them further, and it is certain that stout rhizomes of Water-lilies, and other plants which do not float, are carried along the beds of rivers by undercurrents, so that these non-floating winter bulbils and plantlets may well be carried away.

Lemna (*Lemnaceae*).—Various species of Duckweeds occur all over the world, chiefly in ponds or ditches or slow-moving water. They are almost entirely absent from oceanic islands. I have, however, seen *Lemna minor* brought from Ascension Island; *L. oligorrhiza*, an Australian species, and *L. paucicostata*, a tropical Asiatic species, from Fiji. They are usually absent from isolated ponds or lakes, and I have seen none from the Scotch or Welsh mountain lakes. They are associated more with cultivation areas than wild spots. There is little doubt that they owe a good deal of their distribution to adhesion to birds, especially domestic ducks. They are also carried about by frogs and newts, on the feet of horses and cattle, and in similar ways. In the Malay Peninsula they are to be found, with *Azolla* and *Pistia*, in the ponds made by the Chinese for cultivating pig food, and are thus transferred from one village to another, and to the rice-fields, by adherence to the tame ducks.

From these localities where, if the water is quiet, these plants grow in vast abundance, heavy rushes of water or floods may carry the plants into rivers and so distribute them widely. In 1924 *Lemna minor* had grown very vigorously in the ditch running along Kew Gardens, and in the autumn there was a heavy rise in the river, which invaded the ditch and washed the *Lemna* out. For over a day the whole river was conspicuously green from the vast amount of Duckweed floating down. There must have been many millions of plants.

Pistia stratiotes (*Araceae*).—The Water-Lettuce is very widely spread over the tropics of Asia, Africa and America, and is recorded as found in North America and Southern France in the upper chalk formation. It is absent from Australia and Polynesia and oceanic islands. It frequents backwaters of rivers, and ponds, and in Madagascar occurs in rice-fields. I have seen it floating down the river at Batu Pahat, in Johor, from some locality further north,

and observed that it began to perish as soon as it reached brackish water, and disappeared altogether when it reached salt water. It is reproduced mainly by stolons, and that at a rapid rate, very soon covering a patch of stagnant water. The young plants on the stolons are at first very small, about ½ inch across, and might possibly be distributed by attachment to birds, but I hardly think it likely. The seeds are minute and contained in a berry. According to Klotsch, they germinate on damp shores. In such places they might be easily picked up in mud on the feet of wading birds, or from the surface of the plant by jacanas and such birds as walk on the floating plants. It must be dispersed in some such way, as it is not uncommon in isolated ponds and lakes in Africa and Asia. I have seen it in such ponds in Pernambuco and in the Sitoe Bagindit Lake in Java. It also owes its distribution to some extent to human agency, as it has long had a reputation as a drug, and in Singapore the Chinese carry it about and cultivate it in artificial ponds to feed pigs on. In this case it is usually accompanied by *Azolla*, *Lemna*, and such plants, accidentally adhering to it. I have some doubts as to its being at all indigenous in the Malay region. It, however, is undoubtedly spread over the tropics of the hemispheres, mainly by river and flood.

Azolla (*Salviniaceae*).—These little floating plants chiefly occur in warm and hot regions. There are a number of species, but most are somewhat local. Two species, *A. caroliniana* and *A. filiculoides*, have of recent years spread widely over Europe and most of the rest of the world. They are rapidly diffused by running water, and also to some extent by their adherence to the feathers of water-fowl. The largest species is *A. nilotica*, which is confined to the rivers of the Nile region, where it forms a large part of the Sudd. It is a much-branched fern-like plant, about 6 inches long. *A. pinnata* is a larger plant than the two smaller ones above-mentioned, and it has a comparatively limited distribution, being chiefly found in Australia. I met with it, however, in the rice-fields of Muntilan, near Djokjokarta, in Java, where it had perhaps been carried by birds. The two most widely distributed, *A. caroliniana* and *A. filiculoides*, are among the smallest species. Both were apparently introduced into Europe through botanic gardens, and, escaping therefrom, have spread widely down streams and rivers. *A. caroliniana* appears to have been introduced to the Continent in 1872, and reached England in 1883, France in 1879, and Italy in 1886. It seems to be rare in England, *A. filiculoides*, which much resembles it, having been mistaken for it. It has never been known to fruit in England, and in Europe has only been found fruiting in the South of France.

A. filiculoides, though only introduced in 1880, has spread much more rapidly. The history of the introduction and spread of this plant into Europe has been described by A. F. Marsh (in Proc. Camb. Phil. Soc., xvii, 5, reprinted in the *Journal of Botany*, 1914, p. 209), by W. H. Burrell (*Journal of Botany*, 1914, p. 269), and W. E. Palmer (*Nature*, 1919, xcii, p. 233). It appears that a French botanist, Roze, threw handfuls of both species into ditches at Bordeaux in 1879 and 1880, whence it spread all over the neighbouring country. About 1888 a teacher is said to have procured some from Glasgow and put it into a ditch at Horning Ferry, near the Bure River, Norfolk. Palmer says that he saw it there about 1911, and that the natives of Ranworth hard by said it had been there about 15 years. Heavy floods in August, 1912, carried it up the Bure, the Thurne and Ant rivers. (Palmer called this plant *A. caroliniana*, but Marsh identifies it as *A. filiculoides*.) About the same time it appeared at Queenstown Junction, Cork. It seems almost certain that it was introduced into England before this, but the early records confuse it with *A. caroliniana*. It is now common in many parts of England, and being a popular aquarium plant, often thrown into ponds and ditches, has appeared in many out-of-the-way spots. It is often carried about from pond to pond by adhering to

moorhens and other birds. Unlike *A. carolinianum*, it fruits not infrequently, and this is probably the cause of its being more widely distributed.

In the Straits Settlements *Azolla* is common in the ponds in which the Chinese keep *Pistia* and other water-plants for feeding pigs, and has no doubt been introduced in some of these plants from China, and is often carried about by them in pails with other water-plants. It produces winter buds in the winter in England, which sink into the mud, but may be dispersed by water-fowl. (*See* Bird Dispersal, p. 542.)

Salvinia natans and several other species belong to the same order as *Azolla*, but the plants are larger and very unlikely to be dispersed, at least as whole plants, by water-fowl. They are widely scattered, and, like *Azolla* and *Lemna*, are rather inhabitants of lakes, pools, ditches and stagnant water generally. *S. natans* is widely dispersed in Europe, temperate Asia and India, and I found it in a lake in Java. (Other species occur in America, and *S. oljersiana* in the Bermudas.) It is doubtless carried about by floods and rivers into many of its localities, but as the species often occur in isolated pools, it is probable that their spores are somehow transported by birds.

SUBMERGED PLANTS DISPERSED BY DETACHED PORTIONS.

Elodea canadensis (*Anacharis alsinastrum*) (*Hydrocharidaceae*).—A slender submerged plant, native of North America. It first appeared in Europe in a pond at Dunse Castle, Berwick, in 1842, whence it spread to the Whitadder. Before 1847 it appeared to have been introduced to Foxton, Market Harborough, Leicestershire, in American timber. From here it spread rapidly all over England. In Ireland it appeared at Waringtown, County Down, in 1886. Babington writes that D. Collins says it was introduced into Hampshire with roots of *Nymphea odorata* from America. It was not noticed before these were planted in a pond. Mackay says it was first seen in Dublin with *Aponogetons* and other rare water-plants.

It was perhaps introduced more than once from America in timber and garden aquatics. Only the female plant was known till 1879, when male flowers were found near Edinburgh. Its immense spread was entirely vegetative. Any fragment of it grew with great rapidity, much faster than it does in America, according to Asa Gray. It was carried by river and floods all over England, choking up slow streams and canals, but of late years has become much scarcer. A. Bennett, writing in 1893, said it had gradually become scarcer during the past 20 years. At one time all the ditches were full of this plant; now one has to search for it. It was also largely distributed by attachment of fragments to birds, as described under the section dealing with that subject. (*See* description on p. 537.)

Allied to *Elodea* are the aquatics *Hydrilla*, *Enhydrias* and *Lagarosiphon*, all submerged plants, very similar in appearance. *Enhydrias angustipetala* was discovered by the author in the artificial lake of the Botanic Gardens, Singapore, which was excavated in 1876. The plant grew in enormous masses with great rapidity, so that tons of it had to be removed each year. It also occurred in smaller quantities in ditches and streamlets in Malacca, Perak, Pahang, Siam, Cambodia and Borneo. Like *Elodea*, it grew from small pieces. The plant was certainly not brought to the lake by man, and must have come either by bits from the streams which fed the lake, or by seeds brought down by water or on the feet of birds. With it grew 2 species of *Utricularia* (*U. flexuosa* and *U. exoleta*), also *Naias graminea* var. *angustifolia* (a local variety of a very widely distributed species occurring all over the Old World, the variety only otherwise known from Borneo) and a *Chara*. Many water-birds frequented the lake,

and it is possible that some of these plants may have been brought as seed by them. At the same time there can be no doubt that all of them are from time to time dispersed in the form of floating bits.

Blyxa is a tufted plant with long narrow leaves, inhabiting rice-fields and pools in Asia, and as it has no long floating stems it cannot be dispersed by water, as *Elodea*, but its more or less spiny seeds may be carried about on the feet of birds. However, of *B. echinosperma*, of India, Talbot, in a note in Kew Herbarium, writes :—" At Kanara, at the time of flooding, the deep-" water plants become detached from the bottom and float on the surface." I have seen *B. Malayana*, in the lake of the Singapore Gardens, and in the rice-fields of Malacca, floating in the same way. They could thus be readily dispersed over large tracts of plain country in the rains by floods.

Stratiotes aloides (the Water Soldier) behaves in somewhat the same way. The shoots break off and drift along under water, floating beneath the surface.

Hydrilla is a widely distributed genus, chiefly tropical, resembling *Elodea*, and readily dispersed by floating bits. The only specimen of *H. verticillata* I ever found in the Malay Peninsula was a fragment drifting down the Tringganu River, evidently (as it has not been found again) from a long distance. The plant is very widely distributed all over tropical Asia, and grows in Esthwaite Lake, Lake District, and lakes in Lithuania and Pomerania. It was probably widely distributed over Europe at one time, and has remained only in these isolated lakes.

Lagarosiphon is a similar widely distributed genus in India and Africa. Its seeds are largely dispersed by birds, but there is no doubt it also occurs drifting in floods and rivers in the tropics.

Besides these plants distributed by detached branches borne along by the currents, and continuing to form fresh plants at a long distance from the parent plants, we have many others, such as *Ceratophyllum demersum*, many of the submerged *Potamogetons*, e.g., *P. lucens*, *P. perfoliatus*, *P. densus*, etc., *Naias*, some *Utricularias*, one of which, *U. fluviatilis*, of the Johor rivers, is certainly so dispersed; *Callitriche*, especially *C. stagnalis*, the floating rosettes of which are readily detached and float away in the spring floods; *Aldrovanda*, an aquatic Sundew which inhabits India. Roxburgh (in the " Flora Indica," ii, 112) writes that he " found it swimming in ponds in Bengal. I have never " seen it in other form than detached pieces from 1 to 3 inches long." Branches of the submerged *Ranunculi* (*Batrachium*) are often found floating in the rivers. *R. fluitans* is common in the Kennet, and may be found floating there and in the Thames below Reading as long detached sprays. I have found portions drifted down and stranded on the shores, bearing two or more flowers fully open. In this case the achenes, which are not buoyant when fully developed, could easily be washed down into the river and germinate a long way from the parent plant.

Mrs. Arber notes that in *Peplis portula*, the submerged form, and *Ceratophyllum*, the submerged stems are very brittle, and in early autumn quantities of detached floating shoots may be observed.

Buoyancy of Branches.—As Praeger points out, even if the seeds of a plant have little or no buoyancy, branches carrying fruits may be washed down the rivers, floating for some time. Storms and wind especially, the subsidence of banks, the trampling of animals, may break off and throw portions of plants or even whole plants into the water. He tested the branches or fruiting crowns of a number of plants in water to find their buoyancy. Of 29 plants he tested, the longest floater was *Saxifraga umbrosa*, fresh pieces of which floated for 40 days, dry pieces only 3 days; *Antirrhinum majus*, 15 days fresh, 10 days dry; *Ilex aquifolium*, 14 days fresh and 4 days dry; *Erica*

mediterranea, 13½ days fresh and 6½ days dry; *Rosa eglanteria*, 12 days fresh and 14 days dry.

The plants selected by Praeger were nearly all those which had non-buoyant seeds or fruits, and, except the Mistletoe (*Viscum*) and fresh branches of *Arbutus unedo*, all floated for a day or more. In ten cases fresh branches floated longer than dry ones. Perhaps the most likely plants to benefit by branch flotation are the alpine plants—*Dryas octopetala*, 3 days fresh and 4 days dry; *Sedum telephium*, often a hillside plant, 7 days fresh and 6 days dry; *Alchemilla alpina*, 3 days fresh and 2½ days dry. This is interesting, as I found this latter plant growing on the banks of the Tay, washed down from the mountains as previously mentioned. The heaths, of which fresh branches float from 3 to 6 days, except *E. mediterranea* mentioned above, might be carried thus by mountain streams for some way.

Detached branches of riparian plants are often washed down the rivers, and when stranded on the edges grow rapidly. Many of these plants have non-buoyant seeds or fruits, and their abundance along the river is due largely to this method of dispersal. I have frequently observed this system in the rivers Kennet and Thames.

Among the plants so dispersed are *Veronica Beccabunga*, *Nasturtium officinale* (of which I have found plants so dispersed growing perched on the tops of stumps above the river, having been brought down in spates), *Mentha aquatica*, and *Myosotis palustris*.

Tufts of whole plants growing by river banks are also carried along in floods and, deposited far down the stream, continue to grow. Holmboe (in his " Studies on the Vegetation of Cyprus," p. 231) mentions the drifting of live Tamarisk bushes (*Tamarix* sp.) down the rivers. I have seen whole clumps of *Ranunculus ficaria* and *R. bulbosus*, *Poa annua*, *Carex riparia*, *C. paludosa*, etc., drifted down the River Thames and establishing themselves successfully later on.

The Elephant Grass (*Saccharum arundinaceum*), a huge grass abundant on Malay river banks, is often torn up by a rush of water and carried down stream, to be deposited miles away, and I have seen clumps of Bananas (*Musa*) and Bamboos washed down along rivers and growing successfully when stranded.

In South Africa and Australia the introduced Cacti have been widely dispersed by the drifting of segments of the plant down rivers and in floods. Thus *Opuntia aurantiaca*, thrown out of a private garden into the Kaga River in South Africa after floods, was distributed along the river to its mouth and spread far and wide over the country. *Opuntia decumana* was spread in a similar manner (T. H. Johnston and H. Tryon, " Report of Prickly Pear Travelling Commission, Queensland, 1914 "). Marloth also states that *O. aurantiaca* is widely spread in South Africa by joints of its stems being transported by floods.

Dispersal by Submerged Rhizomes.—Many aquatic and riparian plants have stout rhizomes which, in floods or rapid river spates, are torn up and drifted along, floating till they are thrown up on a mud bank, where they take root and form separate plants. I have seen this occurring in *Nymphaea alba*, *Nuphar lutea*, *Rumex conglomeratus*, *Sagittaria sagittifolia*, *Acorus calamus*, *Iris pseudacorus*, *Typha latifolia*, and *Eleocharis palustris*.

The importance of this method of dispersal is shown in the story of *Acorus calamus* (*Araceae*), the Sweet Flag. This plant appears to have originated in Siberia, whence it was brought to Poland by the Tartars as a drug in the thirteenth century. It was first recorded as abundant in Germany in 1588. It has now spread over most of Europe and many other parts of the world; but in Europe, and, indeed, most other countries, though it not rarely flowers,

it never seems to fruit, or only quite occasionally. It reproduces itself entirely by rhizome. It was long cultivated in Europe, and still is in Asia, as a drug, but in England at least this has ceased for many years. However, it still spreads readily along our river banks, especially in southern England, in abundance, and is not rare in ditches into which its rhizomes have drifted in floods. The wide dispersal and abundance of this plant here are entirely due to the drifting of torn-up portions of rhizomes by floods, rapid rises of rivers, and washing away of the banks.

Sagittaria sagittifolia (the Arrow-head) has a stout but short rhizome, which is washed out in rivers or ditches by a high rise of the water or flood, and floats away. Some years ago a clump of rhizomes of this plant was drifted down the River Thames and lodged in a drain-mouth between Kew and Mortlake. It must have come from a long distance, for I do not know of its growing anywhere nearer than a spot above Hampton Court, about 10 miles away by river. It remained there for several years, the clump increasing in size and developing more leaves, but as it was below high water it did not flower, being often quite submerged. Eventually a very high rise of the river swept it out, and it went further down stream and disappeared. This plant also possesses tubers which can drift down rivers. Mrs. Arber records seeing young plants developing from them in drift at the edge of a river. They are borne on stolons which eventually decay and release the tubers.

Heleocharis palustris.—There is a form of this plant with creeping slender rhizomes abundant in the tidal river from Kew to Barnes. It is habitually submerged, and only clear of the water for a short time at low tide. It hardly ever flowers, and, so far as I can see, does not fruit. It is dispersed by tufts of the plant and its slender rhizomes being drifted down along the bottom of the river.

Bulbils dispersed by Water.—Some of the bulbs of the genus *Allium* are occasionally floated down rivers, but the bulbils in the head of *Allium vineale* sink at once. The leaf bulbils of *Ranunculus ficaria* are dispersed both by rain-wash and river. Mr. Burkill has informed me that he found the bulbils of *Dioscorea* (*Helmia*) *bulbifera* floating down the rivers in the Malay Peninsula. The plant was common at one time in the lowland part of the Economic Gardens, Singapore, and in floods these bulbils could be seen drifting about everywhere. They are round, flattened at both ends, brown, fleshy and warty, from 2 to 3 inches or less across, and are borne in the leaf-axils of the long herbaceous climber. The plant comparatively seldom fruits, and I think is mainly propagated by the bulbils. It is common and widely distributed in the East Indies, being sometimes cultivated as a yam, but is not very popular. It is perhaps this *Dioscorea* sp. which was found on Krakatau after the eruption, as it is abundant in Java, and its bulbils might perhaps have floated across the sea.

In spite of the fact that the bulbils of the Crow Garlic (*Allium vineale*) sink in water, G. W. Wild (*New Zealand Journal of Agriculture*, xxxvii, 1928, p. 23) writes :—" The bulbils may fall into drains and be carried a long way off before " being arrested. The spreading of the Crow Garlic in the area studied (Waikati " district) has been largely effected this way." They are probably carried along in silt.

Winter Buds.—Many aquatics in temperate regions produce condensed tufts of leaf and stem which become detached and eventually form fresh plants. In cold climates this usually takes place in the winter, these winter-buds sinking to the bottom of the water, to commence growth in spring. They may easily be drifted to some distance by undercurrents of water, washed out by floods or heavy spates, and so dispersed. As there is a tendency for many aquatics to produce seed but rarely, this method of reproduction seems to take its place, in many instances, almost altogether.

Hydrocharis Morsus-Ranae (the Frog Bit) produces winter buds in late autumn, which then sink to the bottom of the pool or ditch, and rise to the surface in spring.

Caldesia parnassifolia produces vegetative buds in the inflorescence instead of flowers, dropping the peduncle into the water after flowering.

Utricularia.—In the submerged species of *Utricularia* winter buds are largely produced. Mrs. Arber describes those of *U. vulgaris* thus :—" The tip of the " shoot forms a number of reduced leaves with very short internodes forming " a ball clothed with a layer of mucilage. When the parent plant sinks to the " bottom of the water in autumn, it carries these *turions* with it. They remain " attached to the plant till spring, by which time the connecting stem has " decayed, and these buds float and are readily carried away by the water." Gluck (in a paper on the " *Utricularias* of Great Britain," *Ann. Bot.*, xxvii, p. 616) describes the winter buds of *U. ochroleuca*, a species allied to *U. intermedia.* He says they are found in September and October, and can occur as well on the green floating shoots as on the ground shoots. They are globose, from 3 to 5 mm. thick, and, like those of *U. intermedia*, covered with hair. They begin to grow in May or in the beginning of June.

Thus these plants may be as well dispersed by these winter buds as by their seeds in floods.

Nasturtium lacustre.—Foerste describes (in *Torrey Bot. Club*, xvi, 1889) how this Crucifer reproduces itself by adventitious buds. The pinnately dissected and submerged leaves become detached and float on the surface of the water. An adventitious bud arises at the base of each leaf and develops into a new plant. C. T. Pringle (*Bot. Gaz.*, iv, 237) says :—" It drops its leaves when it " comes into flower, beginning with the basal dissected ones and progressing " up the stem to the small entire bract-like ones. When they alight on the " mud, the bud is produced, and as it grows the leaf decays." These buds have a year's start over seedlings, but he thinks the main dispersal is by seed which is borne away by floods and rainfall. It is, however, probable that, as Foerste suggests, the leaves and bulbils are drifted away by floods.

Cardamine pratensis (the Cuckoo flower) usually grows in wet marshy fields, often in places liable to be flooded. Mrs. Arber describes how she saw countless plantlets growing from detached leaflets in a dyke in the fens near Lakenheath Lode. This seems to be much the same method of dispersal as that of *Nasturtium lacustre.* I have also seen detached terminal leaflets with bulbils floating in the lake in Kew Gardens.

Ranunculus Lingua.—The achenes of this fine Buttercup do not float, but the submerged shoots, after winter, rise to the surface in a rotten state, but bearing healthy buds. These may be carried away by floods and so dispersed.

Myriophyllum verticillatum produces winter buds which sink in the winter and are thus protected from freezing, but in spring may rise to the surface and so be borne away.

Hottonia palustris (*Primulaceae*).—The seeds of this plant sink in water. It is a ditch and marsh plant, with an erect peduncle and finely-cut submerged leaves. In the autumn the stem below the whorl of leaves at the base of the peduncle breaks off, and this portion of the plant drifts away. It is apparently confined to Europe.

H. inflata, of North America, has the peduncles swollen in a succession of internodes with tufts of flowers at the nodes. There are from 4 to 7 of these inflorescences. This plant also appears to break off below the first whorl of its finely-cut leaves.

These plants must depend entirely on the floods to carry them from ditch to ditch.

Movements of Plants in Mass down Rivers.

Sudd is the name given to dense masses of vegetation which, growing in the water of rivers largely from the shallower edges, blocks the channel till portions or the whole mass is torn away by a rise in the river. The masses detached may be carried into other streams, or by flooding into lakes or pools, and so these aquatic plants may be distributed over a vast continent. The sudd usually floats on the river, the water passing under it. It generally occurs in slow-moving rivers in flat open country. It is absent from broad deep rivers, such as the Amazon and Orinoco (Sprague), but is found in the Nile and other African regions, the Ganges, in the Siak River in Sumatra, and in the Essequibo and other Guiana rivers. A good account is given by C. W. Hope (" The Sudd of the Upper Nile," *Ann. Bot.*, xvi, 495), from various sources, of the sudd and its constituents in Africa, India and South America.

In view of the Dispersal of Plants, I restrict the accounts of this phenomenon to facts bearing on this subject only.

In African river the main constituents of the sudd are the Papyrus (*Cyperus papyrus*), *Vossia procera*, a tall grass, and the Ambatch, *Aeschynomene* (*Herminiera*) *Elaphoxylon*, with the buoyant Cyperi *C. colymbetes* and *C. nudicaulis*, and the floating plants *Azolla*, *Pistia*, *Utricularia*, *Ottelia*, *Trapa natans*, *Aldrovanda*, *Nympheas*, and the water fern *Ceratopteris thalictroides*. Hope states that the blocking of the river by the sudd reduces the velocity of the water, and also causes the water of the river to overflow and spill right and left over the country into shallow lakes and lagoons. It is clear that in this way the floating plants may be dispersed into the lakes where there is stagnant water which suits their growth best. An unusual rise of the river may break away large masses of the sudd plants and carry them down stream. He gives an instance of this in the heavy rise of the White Nile in 1878, which carried down enormous masses of vegetable debris that had previously blocked the channel, so that boats took several days to go through. In some cases a rush of water may sweep the contents of the lakes and lagoons into the main river. Sir William Garsten, in his report on the sudd, states he was imprisoned in the Gebel River for three days owing to the sudd having burst in from the side lakes and lagoons and blocked the channel down stream. In the Bahr-el-Ghazal the sudd is chiefly composed of the swimming plants whose breeding places are Lake Ambadi and the other lakes to the south. Here it is clear that the swimming plants are carried into lakes, breed, and are swept out again into the main stream.

Sudd Plants.—The Papyrus (*Cyperus papyrus*) inhabits practically the whole of tropical Africa, from the north of the Nile to Zanzibar, with a form in Palestine. It was introduced into Sicily, it is said, from Egypt in 250 B.C., but the first notice of it is in the tenth century A.D. Bruce found it in Lake Tsana, in Abyssinia, at 5,800 feet altitude. Unless taken there by man, it seems only possible for it to have reached that height by the agency of birds carrying the nuts in mud on their feet.

Vossia procera, a tall grass with thick floating rhizome and branches, forms a considerable part of the African sudd, and occurs, too, in the rivers of India.

Aeschynomene (*Herminiera*) *elaphoxylon* (Ambatch), a leguminous plant. Schweinfurth (in " The Heart of Africa ") writes :—" What, however, most " interested me was the unlimited variety in the kinds of water-plants which " abounded in the floods, the sport of winds and waves. Among them was " *Herminiera*." It shoots up to from 15 to 20 feet in height, and at the base generally attains a thick mass of about 6 inches. The weight of the wood, which he compares to a fungus, is so insignificant that it really suggests comparison with a feather. " The plant shoots up with great rapidity by the quiet

"places of the shore, and since it roots merely in the water, whole bushes are "easily broken off by the force of the wind or stream, and settle themselves "in other places." The Ambatch is allied to the Solah plant *Aeschynomene asperata*, of India, with floating stems, very pithy, and used in making "Solah topi (hats)."

These large sudd plants owe their spread obviously to river-dispersal. Of the minor swimming plants, accounts have already been given, but there is one plant mentioned here which calls for remark—the Water Fern *Ceratopteris thalictroides*. In the African sudd it appears, by the account, to be a floating plant. It is common enough in the Malay region, and is, indeed, one of the most widely dispersed ferns in the tropics, but in most places, so far as I have seen, it is a ditch plant rooted in the ground and does not float at all. It may, however, owe part of its wide dispersal to its floating powers.

Ottelia is another plant which is said to be a floater in the African sudd. The only species I find from the sudd area is *O. alismoides*, which grows also all over Asia, chiefly in ponds and rice-fields in shallow water, but does not float normally. It might, however, be dislodged from the mud by a rush of water and so be dispersed.

Indian Sudd.—The knowledge of this is based on information given by Mr. C. B. Clarke to Mr. Hope, and published in the paper referred to above. Mr. Clarke stated that during the floods the villagers can get about nowhere, except from one village to another—such villages being placed on raised ground—by straight lines kept open through the floating vegetation. This floating vegetation includes *Cyperus cephalotes* and *C. platystylis*, *Aeschynomene asperata*, *Azolla pinnata*, *Ottelia alismoides*, *Vossia procera*, *Trapa natans*, *Pistia*, *Stratiotes*, *Nymphea Lotus*, *N. stellaris*, and *Ceratopteris thalictroides*. *Pistia* is the chief constituent of the rotting vegetation of the Bengal swamps and jheels, which forms a buoyant mass from 6 to 24 inches thick. The whole of the rice-field weeds may grow on such masses, and seedlings of trees such as *Bombax* and *Erythrina* sometimes appear plentifully on them.

In the Siak River, Sumatra, there is said to be almost impassable sudd consisting mainly of *Susum anthelminticum* (*Flagellariaceae*). I do not think any naturalist has yet visited this locality.

Malay Peninsula Sudd.—Though the rivers here are hardly large enough to produce sudd to any extent, yet in the Pahang River we have large quantities of vegetation brought down through the sandy plains of the eastern coast. As the water travels, from time to time islands are formed, on which trees and shrubs, as well as herbs of all kinds, are brought down by spates and deposited. Eventually a heavy flood of water comes and washes the whole island away, redepositing the sand and many of the plants unharmed some miles down the river, and this goes on till the island, with its vegetation, at last reaches the sea and disappears. Frequently in these sandy plains the river changes its course, and many villages, still called islands, are now a long way from the river, though originally in the middle of it. In such cases, not only seeds and fruits, but bushes and small trees, clumps of bamboo and bananas, may travel unharmed for long distances, and eventually perhaps form the nucleus of a forest if the river shifts its course.

South American Sudd.—This is described by J. Rodway (in "In the Guiana Forests") and quoted by Hope. Here, when the water in the rivers Essequibo, etc., is low, the extensions of vegetation grow out from the bank till they nearly meet. These extensions consist of *Montrichardia arborescens*, a tall aquatic aroid, and a grass, *Panicum elephantipes*, while several Leguminous bushes—*Drepanocarpus lunatus*, *Ecastaphyllum Brownei*, and *Muellera moniliformis*—grow out as far as they can from the bank. When the floods come, these vegetative extensions are torn away, and large masses 50 feet or more in diameter

are released. Occasionally a very obstinate obstruction will withstand the flood and cause the washed-down material to become an impenetrable barricade, so that the river's course is shifted by the washing away of the further side, and a new bend in the river is formed.

The Aroid *Montrichardia* establishes itself where it is sufficiently shallow, and eventually an island is formed. Here the sudd—or, rather, the blocking of the river—is quite different from the sudd of Africa or India, as, owing to the density of forest, there are probably no open plains where the typical floating vegetation can be evolved. *Pistia* and some other floaters occur in these rivers, but not in sufficient quantity to play an important part. Though undoubtedly the *Aroid* and the *Panicum* are here water-dispersed to some extent, the rest of the washed-down vegetation fails to establish itself and is destroyed, either broken to bits by the rush of water, or carried down to the sea-beach, where it perishes. Guppy, in writing of the beach-drift of South America, mentions a large number of seeds and fruits brought down by river, including those of *Ecastaphyllum* and *Drepanocarpus*, and doubtless the seeds of these trees and shrubs in many cases develop into adults along the river bank (though many perish in the sea), and also form the ever-increasing forest on the land developed by the silt of the mountains. Spruce ("Notes of a Botanist," i, 506) writes of similar drift in the Amazons. "The Ilhas de Caapim, Grass Islands, I find, are "floated out of lakes by the rising of the waters of the Amazon, which thus "fulfil the double purpose of calling certain species into existence, and afterwards "bearing them away to the ocean. The chief, and often the sole, constituents "of the grass islands are the wild Sugar-cane and the Brittle grass, *Panicum* "*spectabile* and *Paspalum pyramidale*. For the production of these plants white "water is essential. Lakes are usually of black water, but those lakes into "which white water enters during the rainy season invariably produce these "two grasses, sometimes in such abundance that they become periodically "choked up." He describes one of these floating grass islands in the Solimoes, consisting only of the *Paspalum*, of which one stem measured 45 feet, and says, "floating on the water and kept in by the grass stems were an "*Azolla*, two *Salvinias*, a few barren plants of a *Hydrocharidea*, and a small *Pistia*."

FLOATING SEEDLINGS.

Some riparian and marsh plants whose seeds are not buoyant have the habit of germinating when sunk in water, and then the seedlings, floating to the top, are readily borne away by a stream or river, to continue their growth when stranded on a suitable spot. They may also be drifted along on floating sticks and other such debris, and Mr. Dymes tells me that Woodruffe-Peacock has observed seedlings borne along on the plumage of wild duck.

The number of cases in which I have known this method of dissemination to occur is small, but I have little doubt that it is a much more common occurrence than is supposed, for there are a number of riparian plants, as well as aquatics, in which the seeds certainly sink, yet these plants may frequently be seen moving along river banks.

In marine and littoral plants this form of distribution is more conspicuous, and more common proportionally to the number of species. The *Rhizophoraceae*, *Avicennia* and *Aegiceras*, habitually adopt this method of dispersal, as do also the submerged marine plants. These, however, are dealt with under Sea-Dispersal. *See* pp. 287–290.

Mimulus luteus.—In this plant the seeds float for a few days and then sink as soon as they have absorbed water. After remaining at the bottom of a jar for about a week (in one case from September 23rd to October 1st) they

germinated and rose at once to the top of the water. The seedlings floated on the surface till February. Some which were frozen in ice during that period survived, but most of them perished. This plant was introduced into Europe from North America, and is commonly cultivated in gardens, and has spread very rapidly along streams in England and Scotland, becoming extremely abundant in many places. I observed that, when grown on land, it spreads rather slowly. The very minute seeds, when dispersed by the wind shaking the plant, seem to go no more than 3 feet away from the mother-plant, and come up around it in large patches, but most of the seedlings then perish.

Primula japonica.—This Japanese Primrose is recorded on tickets in Kew Herbarium as inhabiting inundated meadows. Indeed, in cultivation it seems to do best in wet ground. The seeds are minute, with a hard, thick pustular testa. They float for a week, then sink, and afterwards germinate and float. I found they floated from August 4th to August 13th, but some began to germinate on August 12th, and nearly all had germinated by August 13th. They were still floating on October 13th. It is clear that in flooded meadows they might be very readily dispersed to a considerable distance.

Stachys palustris.—In this the nucules float apparently from an air-space between the seed and pericarp. In water they germinate in a week, and the seedlings float.

Scrophularia aquatica.—The dissemination of this river-plant, obviously by water, puzzled me, as the very small seeds sink immediately. Seeds put in water, however, sank and remained at the bottom for about a week. They then germinated under water and emitted the radicle, but did not float for two days—that is, when the cotyledons were expanded. This took place in August, and the seedlings were still floating on October 13th. It is undoubtedly due to the floating seedlings that this plant makes its way along the river edges.

Echinodorus ranunculoides.—The little achenes sink at once and germinate below the water in about a fortnight. The seedlings floated from August 28th to October 23rd.

Lythrum salicaria.—The seeds of the purple Loosestrife soon sink on being thrown into the water, but after a week they germinate at the bottom, and float on the surface in the same way as those of *Mimulus*. I noticed that, after germinating in a glass jar, some speedily came to the top, while others remained at the bottom till air-bubbles appeared, which brought them to the top and kept them there. The plant is a riparian one, and I have observed it gradually moving down the river at Kew towards Mortlake, no doubt disseminated by the floating seedlings.

Aster tripolium.—Guppy records the floating of the seedlings of this plant. I put 3 achenes, apparently ripe and in good condition, into a jar of water on February 8th, 1928. They all sank to the bottom on February 15th. On February 22nd one germinated, spread out its cotyledons, and floated in good condition, making a slight growth till March 7th, when I took it out of the water and planted it.

Medicago lupulina.—Fruits of a plant from below high-water mark at Kew, October 13th, sank, germinated October 21st. Seedlings floated till November 3rd, when free of testa.

Salicornia herbacea.—The seeds of this little sea-mud plant sink in water. They germinate when sunk in sea-water or fresh water, but more readily in the former, the sea-water seedlings being the more vigorous and healthy. Guppy kept the floating seedlings in sea-water for about 10 weeks after germination, by which time they had developed the second joint and rootlets. After that they became sickly, and died unless placed in salt mud. This is what might have been expected. The seedling cannot become an adult plant while floating. Much the same thing takes place in *Mimulus luteus*.

There can be no doubt that this is the method of dispersal in this plant. The plant is common on the European and North American coasts, and occurs in Bermuda and on the Vancouver Islands.

Probably most of the other species are distributed in the same way. Guppy mentions *S. peruviana* as a South American species (as tall as a man) of which he has found germinating fruits floating in the drift of the Guayas River, Ecuador. He also mentions finding the seeded joints of it floating in the Guayaquil River. This plant is found in the West Indies and Juan Fernandez, as well as in Ecuador and Peru. Other species occur on the coasts of India, Ceylon, Formosa, Liukiu Islands, Australia and New Zealand.

Mr. T. A. Dymes writes me that the seeds of *Iris pseudacorus* will float of themselves for from 18 months to 2 years, and after sinking will rise to the surface of the water after germination and float again. The achenes of *Ranunculus sceleratus* sink after a few days, but some seeds germinate and float, others rise again after germination. He is of opinion that in these cases it is a matter of unfavourable hard soil. If the seed cannot anchor itself by the radicle, the seedling will rise.

Hottonia, he says, seems to raise its seedlings deliberately by secreting a bubble of air between the two small cotyledons. At times, especially in spring, air-bubbles rise from the mud of ditches and pools and uproot seedlings. He has seen this occur with *Iris* also.

Juncus.—The minute seeds of at least some of these plants exude mucilage when wetted. I put the seeds of *J. Chamissonis* and *J. glaucus* into a jar of water, and they sank in a day, probably after absorbing water. A week later they began to germinate, and the seedlings floated up to the top. The single cotyledon is a green, slender, worm-like terete body with no visible hypocotyl, but with a transparent root with root-hairs. The testa of the seed remains attached to the cotyledon when it floats. The seeds of all the *Junci* are non-buoyant, and sink at once, or very soon, in water. Anyone, however, must be struck by the way the tufts of *Juncus communis* and *J. effusus* fringe the runnels in wet meadows, as if the seeds had been borne along and stranded. In some cases I have no doubt that they are carried in silt under water and thrown up with the silt, but there are many cases in which this could not occur. I find plants of *J. effusus* on the river bank at Kew between the stone setts of the embankment, above any position where silt can have reached. The plant does not grow in the immediate neighbourhood, and cannot have reached its position by the action of rain-wash on the seeds, nor by the drifting of a rhizome, nor is it at all probable that it is brought there in mud on the feet of birds. I can only conclude that they have been drifted down the river from a long distance in the state of seedlings.

Al. Borza and Gh. Bujoreau give an account of a number of seeds which they immersed in sea-water in the Black Sea, and of which some germinated and the seedlings floated. Among these were *Lepidium ruderale*, *Stellaria media*, *Portulaca oleracea*, *Matricaria inodora* and *Bromus hordeaceus*. None of these are marine or even littoral plants. Guppy tried immersing a number of seeds in sea-water from 6 to 33 months, and the greater part of the inland species failed to germinate. He says that in nearly all the plants that failed to germinate in sea-water the capacity of readily germinating in fresh water was displayed. He noticed that a previous immersion in sea-water favoured early germination in fresh water. The importance of the germination of non-buoyant riparian seeds in fresh water, and their dispersal as seedlings, seems to have escaped him. Most of the plants he tried had buoyant seeds, but, curiously enough, included in them were several species of *Junci*, most of which germinate rapidly in fresh water, and to this they owe their dispersal.

Of littoral plants whose seeds germinate in the water, he mentions *Aster*

tripolium, *Salicornia herbacea*, *Spergularia marina*, *Triglochin maritimum* and *T. palustre*, and *Batis maritima*. Of these, as might be expected, after germination the seedlings made but little attempt at growth while floating in sea-water, except in marine plants like *Salicornia*. This germination in sea-water by tidal mud-plants like *Aster tripolium* might play an important part in their dispersal, as seedlings might be drifted from creek to creek, and after being carried up into less saline waters by a rising tide, might establish themselves up river. Darwin found that seeds of *Tussilago farfara*, *Convolvulus tricolor*, and the garden *Orache* (*Atriplex hortensis*) germinated under the water and lived there for some time. The Mangroves *Rhizophora*, *Bruguiera*, *Rheedia*, *Laguncularia* and *Avicennia* and *Ægiceras* habitually germinate in the sea, or on the branches of the tree, falling into the water to continue their development, and *Batis* is also germinated in the sea, but I refer to all the strictly marine plants under Sea-Dispersal.

The germination of seeds which sink in fresh water and then float to the surface and are dispersed as seedlings by water currents, is a matter of great importance to riparian plants, and much more research on this line is required.

HEAVY SEEDS DRIFTED UNDER WATER.

The dispersal of certain river-bank and seashore plants of which the seeds sink in water at once, and which do not possess rhizomes or branches by which they could be floated along, is somewhat puzzling. In some cases the question has been solved by finding that the sunken seeds germinate at the bottom of the river or sea, and, floating, are dispersed as seedlings. I believe that in some cases sunken seeds may be washed under water by currents, and eventually thrown up with silt, sand, or gravel. Both rivers and sea throw up sand and stones in floods or storms much higher than one would expect, and if these heavier materials are thrown up, it would be equally natural for sunken seeds to be thrown up also.

In the sea the possible movement of heavy seeds would be restricted to comparatively shallow depths, as it is not probable that, if once sunk to a great depth, material could be raised again by currents.

J. S. Owen made some experiments on the transporting of sand and stones by sea-currents, and read a paper on the subject (published in the *Geographical Journal*, 1908, p. 15). His experiments were made in comparatively shallow water, but wave action seemed to be effective to a depth of from 30 to 40 fathoms. How much could be done by deep basal currents is obscure, but it is probable that seeds could be drifted along under water and washed up with sand.

I give an instance in which it appears that the heavy seeds of *Glaucium luteum* have travelled in this way. The Horned Poppy is found in Swanage Bay at the furthest north point, Punfield Cove, on sandy soil. It has been there very many years. The plant occurs in Studland Bay, but between the two bays is the long projecting chalk ridge, Ballard Down. On the south and west side of Swanage Bay the plant is quite absent as far as Kimmeridge Bay, a distance of 10 miles. Indeed, no part of this coast between these points is at all suited for its growth, being all high cliffs. A local fisherman told me that the currents in this part of the sea ran from Durleston Bay into Swanage Bay, not from Studland Bay, and that these currents brought great quantities of sand and shingle from the south, sufficient sometimes to fill the lobster-pots. I observed in Punfield Cove that there was a quantity of shingle, evidently of Purbeck and Portland rock, from Durleston Bay, which was absent from the rest of the harbour. It is clear that if the sea could carry along stones of this size with the

sand, it could also carry seeds of *Glaucium*. If, as appears probable, the seeds came from the south coast, they must have come from Kimmeridge Bay, which would be a very long distance to travel safely along the sea-bottom. *Glaucium luteum* is missing from such islands as the Canaries and Azores, and it may be presumed that if the seeds sank or were carried into deep water, they would not be washed up again. The question remains as to how long these seeds could stop under water in the sand at the bottom, and then be washed up and germinate. Of this, in the case of this plant, I have no evidence, but in the case of *Eryngium maritimum*, Martins kept 20 seeds in sea-water for 40 days, of which 11 germinated later.

WASH-OUT OF BURIED SEEDS.

Certain seeds, especially of Leguminous plants, can remain buried for many years and yet germinate when dug up and put in suitable spots. Frequently the original plant has quite disappeared from the area, but its buried seeds may be turned up by the plough or spade, and the plant eventually reappears. This is equally well effected by water. A river changing its course may wash out the soil in a plain, bring to light and carry along seeds which have been long buried, and deposit them in a position where they can grow. In this way seeds which were too heavy to float may be washed out with the earth and stones, and so be dispersed by the river. This may account for the distribution of many marsh or damp-land plants, the seeds of which are too heavy to float.

I mention here a paper by J. Salter on the vitality of seeds after prolonged submersion in the sea, in which he records the occurrence of certain plants on mud dug up in Poole Harbour (Proc. Linn. Soc., i, p. 140), though I have great doubts as to his conclusions. He found that on the mud appeared large quantities of Oats and Barley, some *Lysimachia vulgaris*, *Centaurea calcitrapa* and *Epilobium hirsutum*, none of which grew in the neighbourhood. The mud had been dredged into ballast barges and then spread over an area and left undisturbed. Now, these cereals never appear as abundantly as they are supposed to have done in this case, unless they are in the neighbourhood of grain stores or where horses are used. The grains very soon perish in wet spots or the sea. There can be little doubt that they were either thrown out with the mud from barges formerly used for grain, or from the nosebags of the horses presumably used when distributing the mud. *Centaurea calcitrapa*, of which one plant only was found, is frequently distributed in grain. *Epilobium hirsutum* was growing 2 or 3 miles away, and might easily have been carried that distance by wind. *Lysimachia vulgaris* may possibly have been washed down to and sunk in Poole Harbour, and afterwards excavated and strewn out on the mud. Although this instance of Salter's is not good evidence of the durability of seeds in tidal river-mud deposits, still it is extremely probable that certain seeds may be so deposited, and later freed so as to germinate, by river-wash as well as by human interference. It seems probable that the Leguminous plants *Cassia siamea* and *Albizzia stipulata* in Krakatau survived the rain of ashes from the volcano, and later, washed out by denudation, germinated and established themselves there.

When clearing some ground in the Singapore Botanic Gardens, the climbing *Euphorbiaceous* plant *Pterococcus glaberrimus* suddenly appeared. The ground had at one time been under Chinese cultivation, later abandoned, and for many years covered with the Lalang grass. During the work of clearing and digging, this plant came up. It is quite rare in the Peninsula, and was possibly only found there as the remains of cultivation, as it is occasionally used as a vegetable. (I have never, however, seen it in cultivation.) The seeds are very hard and may last a long time in the ground. It is of some importance to bear

in mind that buried seeds of a plant long lost may reappear and grow when exposed by turning over the soil, or by being washed out by river or stream, and this may be the cause of the unexpected appearance of a plant in a new locality.

Through the kindness of Mr. C. Mosley, of Huddersfield, I have been able to procure a copy of a note on the appearance of *Convolvulus arvensis* on the banks of the River Colne, laid bare by the falling of the river. The seeds of this plant are non-buoyant and sink at once. I can only suggest that the seeds had at some time fallen into the river, sunk, and been covered with mud, germinating and growing only when the river had fallen low enough to expose them.

" *Dispersal of Seeds of Corn Bindweed.*—A striking example of the dispersal " of seeds by water was afforded last year (1901) on the banks of the River " Colne, at Damside, Huddersfield. Owing to the continued dry weather, " the river receded from its banks to a great extent, and on the patches of land " thus left bare in this particular locality a large portion was soon made gay " by the foliage and pretty cup-shaped bloom of Corn Bindweed (*Convolvulus* " *arvensis*). Nothing has grown on this particular piece of ground when laid " bare for shorter periods in previous years—at least, not during the past " fourteen years to which I can testify, and it will be interesting to note whether " the plant will again appear another year from the seeds which have fallen. " By now the winter rains have swept the plants away." (Copied from *The Naturalist's Journal*, Jan., 1902. The writer of the above note is Mr. W. E. L. Wattam.

It is obvious that heavy seeds might fall into the water and sink, and be rolled along, at least in rivers, quite as easily as stones and silt, and be thrown up with these on gravel banks, shingle, or dry mud, and if the river shifts its course, these seeds might, on being exposed, germinate and grow. They might also be covered with mud for a considerable time, and on the drying up of the mud, might appear, and the same might happen to submerged rhizomes of aquatic plants. A pond in the Singapore Gardens which, some years before, I had excavated and planted with Water-lilies, became in time so completely silted up that it was nearly a dry piece of ground. The Water-lilies had long disappeared. I had it re-excavated and allowed to fill up again with water, and in a surprisingly short time it was dotted over with the Water-lilies again. Here the rhizomes must have remained buried in the mud for some years, but still alive. Had a river cut through the swamp, it might have brought these rhizomes to light again and carried them further away.

FLOATING SEEDS AND FRUITS.

Adaptations for Dispersal by Floating.—The modifications of fruit or seed for purposes of flotation is the subject of an important paper by Ravn (" Sur le faculté de flotter chez les graines de nos plantes marecageuses," *Botan. Tijdschs.*, xix, 143, Copenhagen, 1894). Of those of maritime plants we have researches made by Schimper (" Strandflora ") and Guppy.

In some cases the whole fruit floats, and in this case the fruit is usually 1-seeded. There are, however, some many-seeded fruits which float, such as *Hodgsonia capniocarpa*, a woody gourd, round and flattened, covered with a thin plush-like fur which is not wetted by water. It is a native of the river banks of Malaya. When the fruit breaks up, the numerous large oily seeds also float. There are others of the *Cucurbitaceae*, *Luffa* and *Lagenaria*, the fruits of which float, as does also the berry of the Hawthorn (*Crataegus*) though it is certainly more commonly dispersed by birds and rain-wash than by stream or river.

But most of the floating fruits are 1-seeded, the pericarp, calyx, or bracts being the actual buoyant parts. Many seeds of capsules or berries are to be found floating, and are so dispersed.

Praeger's figures for buoyancy not unfrequently differ from those of Guppy, but the latter shows in many parts of his work that there is a great variability in the buoyancy of seeds and fruits of the same species, some seeds and fruits floating much longer than others. Inland-growing plants seem to have a tendency to produce heavier fruits and seeds than those growing on river banks and seashores, but even in the same capsule we often find seeds which sink at different dates. Guppy estimates that of British fruits and seeds 60 per cent. sink immediately or within a week, 25 per cent. float for a month or more, and 15 per cent. float for over 6 months, and says that it is to this last small group that belong the seeds and seed-vessels which float through the winter in our ponds and rivers. He examined a few grasses, in many of which plants, the grains, though non-buoyant themselves, are transported in their glumes, in which they are sometimes quite enclosed and which contain a certain amount of air. Praeger gives, as a result of his experiments, 85·2 per cent. as sinking in 1 week, 5·2 per cent. floating from 1 to 4 weeks, 3·3 per cent. from 1 to 6 months, 1·9 per cent. from 6 to 12 months, and 4·4 per cent. over 12 months.

He gives a table of buoyancy (arranged according to habitats of the plants) showing that of the water-plants (aquatics), marsh plants possess the greatest seed- or fruit-buoyancy, over $\frac{1}{2}$ the total; maritime plants $\frac{1}{7}$ the total; bog plants very little; dried fleshy fruits a small proportion, and none of these float over 6 months. The balance of the buoyant seeds is made up of plants of various habits and habitats.

In his list of Britannic plants Praeger has recorded cases where the floating periods of seeds are less than a day—for 12 hours only. Even this short period may be of importance to a plant, as if it falls into a rapid-moving current it may be transported to a considerable distance before it sinks or is stranded. *Cryptocoryne ciliaris* is a tidal-mud Aroid, abundant in the tidal rivers of the Indo-Malay region. The fruits are capsules containing a number of round seeds which commence to germinate under water (or raised just above it), before the capsule opens. When the seeds fall or float out, the cotyledon has developed into the form of several narrow dark green linear segments at the end of the seed, and by this floating organ the seed is drifted away. After a few minutes, however, the cotyledon becomes detached and the seed sinks at once into the mud. The few minutes (for it is hardly more) in which the seed is floating on a rising or falling tide would be sufficient to carry it to a considerable distance from the parent, at the same time avoiding the risk of its being carried out to the open ocean, where it might eventually sink or be stranded on a sand-bank or gravel beach, where it could not grow.

A number of the seeds and fruits which float a short time are those of inland plants, which rarely require the act of dispersal by water, their buoyancy being adventitious. Most fruits or seeds adapted for wind transport will float, and such plants may be widely diffused by floods and heavy rushes of water. Such plants as *Salsola Kali* and *Xanthium strumarium*, though not river-bank plants nor the inhabitants of swamps, owe a great deal of their distribution to the rush of flood-water over large areas. *Dolichandrone Rheedii* and *Casuarina equisetifolia*, both plants with modifications for flying, in the form of wings to the seed or fruit respectively, are more widely disseminated by water than by wind.

Many seeds which I have tested, though not really buoyant, will float till they get thoroughly wetted, when they sink.

In still waters floating seeds are much assisted by wind blowing over the surface, and in pools or lakes where numbers of floating seeds or fruits (e.g., Alder and Birch) fall in, these may be found in large quantities driven to the shores by the wind and there stranded by the fall of water. A number of seeds fallen into the water and lodging on dead sticks or floating leaves, or embedded in *Confervae*, are often carried along in rivers.

Bracts as Floating Organs.—The modification of bracts as floating organs is mainly confined to Grasses and *Carices*. In many grasses the glumes (bracts) remain, persistently enclosing the grain when ripe, and when the grain is blown by the wind, or accidentally falls into the water, it floats in the boat-like glumes, which enclose a small quantity of air in the space between the glume and the grain. In the tall riverside grass *Coix gigantea* the female spikelet is enclosed in a bony, hard white bract. There is only one grain in the spikelet, and when fallen, it floats away in the river. The plant is an inhabitant of river banks in tropical Asia. The common species, *C. Lachryma-Jobi*, owes its world-wide distribution mainly to man, being cultivated as a cereal or curiosity, but it was probably originally a river-bank plant, as it has the same structure as *C. gigantea* (Pl. XII, figs. 9 and 10).

In marsh and river-edge grasses, such as *Leersia oryzoides* and other species, *Oryza*, *Glyceria aquatica*, *Digraphis arundinacea*, and probably many others, the grains, enclosed merely in their glumes, float away when they fall into the water, as mentioned above, and in many *Carices* the utricle (a modified bract enclosing the small nut) contains enough air to float it along a stream or river. *See also* Seeds and Fruits Dispersed by Water, pp. 238–240.

Buoyancy of Fruits Due to the Sepals or the Sepaline Tube.—This occurs in many fruits in which the ovary is securely enclosed in the tubular portion of the calyx, as in *Compositae* and *Umbelliferae*. In such fruits the outer tube consists of an aeriferous tissue forming a layer over the whole fruit, as in *Bidens tripartitus*, *Cicuta virosa*, *Oenanthe*, *Terminalia catappa*, *Lumnitzera* and *Guettarda*.

Sometimes the persistent, and often accrescent, sepals are the floating organs, as in *Isoptera* (*Dipterocarpaceae*), in which the sepals form a flat corky plate supporting the round fruit.

In the Docks (*Rumex*) the sepals are usually provided with a corky boss on one or more of them, which aids to float the nut. These corky tubercles only develop as the fruit is ripening. If they are cut off, the fruit sinks. Other modifications of the calyx for floating are to be found in the *Eriocaulons* and in the extraordinary hollow sepaline cup of the littoral *Hernandia ovigera*.

The Pericarp as a Floating Organ.—Many fruits, especially the larger ones, owe their buoyancy, and consequently their wide distribution, to the lightness of the pericarp, or wall of the ovary. In the Coconut (*Cocos nucifera*) the outer husk is fibrous, very light, and full of air, and the testa of the seed very hard and bony, and the fruits of the Nipa Palm and *Pandanus* are very similar, though the husk is less thick. The outer layer of the pericarp is smooth and polished in these fruits, and resists for a long time the decay caused by the action of sea-water. In *Scirpodendron* and *Sparganium* the pericarp is corky and very light. It is composed of air-cells with thin walls and large intercellular spaces. The seed sinks at once when the husk is removed. *Cladium*, a very widely distributed Sedge, has a similar but thinner corky coat. The same principle is also found, according to Ravn, in the nutlets of *Mentha aquatica* and also in the sea-dispersed *Tournefortia argentea* and *Mertensia*. In *Lycopus europaeus* the nutlets are partially surrounded by a corky ring by which they float.

In *Pontederia* the pericarp is fleshy, but contains aeriferous tissue. The raceme of fruits, when ripe, is bent down into the water, and the fruits float

away. After a short time the soft, green fleshy pericarp decays, and the seedling splits it and escapes to sink in the mud, where it takes root.

This system of the thickening of the light pericarp with aeriferous tissue or air-spaces between the cells, or both combined, is the most common method of modification of fruits for dispersal by floating in river or sea. Usually, after a time, the outer coat of the pericarp decays in the water, and the seed sinks. This may take days, weeks or months, according to the structure of the pericarp and its power of absorbing or resisting the absorption of water. In submerged plants the period is often short, as there is otherwise a risk of the seeds being stranded on an exposed bank, where they would fail to germinate.

For inland plants, or those of river banks, it is important that they should not float too far, as they might be carried into the sea and lost. It is due to the fall of the water that the seeds of plants dispersed by floating become stranded in spots favourable for growth. The rise in the rains, or flood-time, conveys them to the banks and river edge, the fall of the water leaving them to grow. When once rooted, the little plants are not affected by any rise of water which may temporarily cover them.

In many small fruits the thin pericarp consists of aeriferous tissue. Such are those of *Scirpus maritimus*, *Blysmus compressus*, *Potamogeton*, the fruit-carpels of *Ranunculus sceleratus* and nutlets of *Scutellaria galericulata*. Ravn points out that the fruit of *Blysmus rufus* has no air-tissue like that of *B. compressus*. It is dispersed over saline marshy grounds by flood only. It is interesting to note that *B. compressus*, a stream-side and open swamp plant, is more widely distributed than *B. rufus*. Ravn says that the air-tissue in *Ranunculus sceleratus* and in *Alisma plantago* is sub-epidermal. This is also the case in many of the other fruits with pericarp buoyancy.

In *Sagittaria* the carpels have wings of light air-tissue, as well as a large-celled light epidermis, and the seed is light compared with the extent of the wings. These are even larger in *Lophiocarpus guyanensis* of the tropics. The edge of the carpels of *Alisma plantago* have also dilated thin margins.

In some fruits the buoyancy is due to the fact that the seed does not fill up the whole of the capsule or pod, so leaving an air-space sufficient to float it. This is not uncommon in the pods of the *Leguminosae*. In these buoyant pods, as a rule only one seed is developed. Such are those of *Dalbergia monosperma*, *Derris uliginosa*, *Inocarpus edulis*, *Pongamia glabra*, and *Cynometra*. They have tough, parchment-like or woody pods, with a seed which almost invariably sinks at once. In some other *Leguminosae* the many-seeded pod is jointed, and the joints break off separately and float freely in the river or sea, each joint containing a single seed. Such are *Desmodium umbellatum*, *Derris sinuata* and *Aeschynomene*. Some other plants have fruits with the same class of modification for buoyancy—*Heritiera*, with its thick, corky fibrous pericarp, *Gyrocarpus*, *Smythea*, etc.

In *Albizzia* the thin, flat wind-dispersed pods can float for some time, from the large proportion of thin pericarp to the comparatively light pod filled with a loose pithy tissue, which, when dry and full of air, is sufficiently buoyant to float the heavy seeds.

Among other methods of modification for buoyancy we may include the bladder-fruit system, in which the walls of the capsule are thin and dilated with air, so as to readily float the seeds on the rivers and allow them to be blown along by the wind. Such plants as *Dodonaea*, *Cardiospermum*, *Sutherlandia*, etc., are so dispersed. In another form of fruit the buoyancy is due to the suppression of some of the seeds, leaving empty cavities. Such are those of *Premna tahitensis* and *Dichilanthe*. In some drupes, *Ximenia americana* and

Calophyllum, the kernel is light enough to float, but there is also a layer of air-bearing tissue beneath the shell.

Buoyancy of Seeds.—The floating power of seeds is due either to the lightness or buoyancy of the kernel, or from the buoyancy of the testa, or occasionally from both combined.

(1) Buoyancy of the kernel may be due to actual lightness of the albumen, as in *Crinum*.

(2) By the lightness of the cotyledons, as in *Lathyrus maritimus*, *Dioclea*, *Strongylodon*, *Canavalia*, *Erythrina*, *Sophora tomentosa*, and other *Leguminosae* and *Honckenya peploides*.

(3) It may be effected by spaces left between the cotyledons. Thus in *Hibiscus tiliaceus*, *Thespesia*, *Suriana*, *Ipomoea*, *Colubrina*, the cotyledons are foliaceous and crumpled irregularly, or folded so that the testa is not completely filled, and spaces are left, by which the seeds are buoyant.

(4) There may be a central cavity between the two cotyledons, which are large and flat, and which, when ripe, shrink away from each other. *Vigna lutea*, *Mucuna*, *Guilandina bonduc*, and *G. bonducella* and *Entada*, have this form of seed.

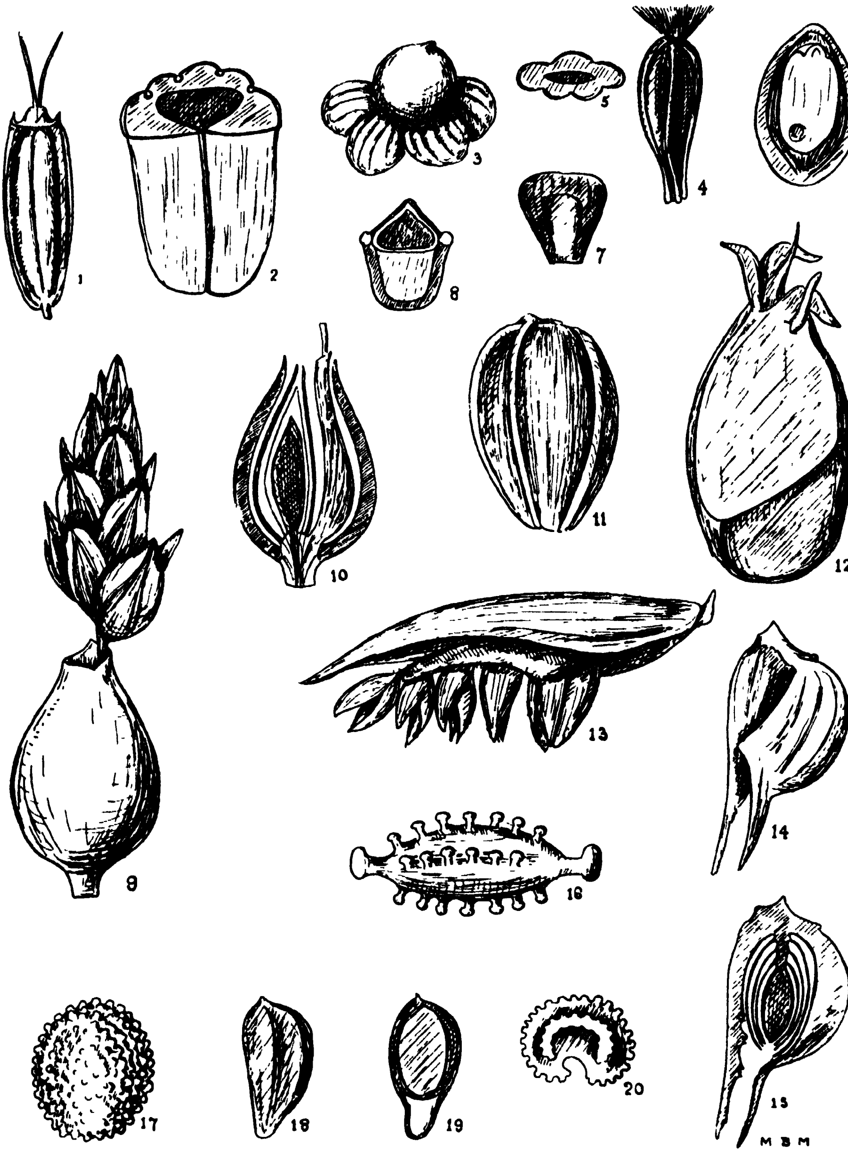
In neither of these last two groups are either the kernel or testa buoyant, but sink at once when the seed is opened up.

Buoyancy of the Testa.—In many of the seeds, especially of sea-borne species, the testa is corky and made of light aeriferous tissue. Such are the large seeds of *Carapa*, and the small ones of *Pemphis*, *Sonneratia*, and *Cakile maritima*. In the seeds of the Water Flag (*Iris pseudacorus*) the outer layer of the testa is thin, but made of aeriferous tissue; it causes the seed to float, and when in the spring it decays, the seed sinks. In *Menyanthes trifoliata*, *Scheuchzeria palustris*, *Calla palustris* and *Lemna* the testa consists of aeriferous tissue with inter-cellular air-spaces. The seeds of *Pedicularis palustris* are similar, but there are no air-spaces. The testa, though hard outside, may have a buoyant tissue beneath the hard outer layer. This occurs in *Mucuna gigantea*, *Excoecaria Agallocha*, *Anona palustris*, *Euphorbia paralias* and *Cycas*. In the Marsh Marigold (*Caltha palustris*) the floating organ is unique. It consists of the persistent swollen raphe and chalaza.

Variation of Seed Buoyancy in the Same Species.—It is clearly shown that seeds and fruits of the same species of plants often vary very much in their buoyancy. If 20 per cent. of any seeds or fruits float and the rest sink, it is clear that only the 20 per cent. could establish themselves as riparian plants, and only the seeds of that 20 per cent could hold their own on the river bank. Any seeds produced which were too heavy to float would be at once eliminated. Guppy shows also that inland plants may be evolved from plants whose seeds have arrived at an island by sea transport, and thus necessarily have buoyant seeds, and that these inland-evolved plants have seeds which are no longer buoyant, but sink in water. This is a very remarkable fact in evolution, and requires further investigation.

In testing the floating capabilities of various kinds of seeds and 1-seeded fruits, I have found in several cases that on throwing the seeds (all apparently equally sound and from the same plant) into water, a certain proportion always sank at once, but of the remainder, some of them floated, and for a considerable period. Among these were the winged nutlets of the Birch (*Betula alba*), which Guppy classes as non-buoyant. Some of the nutlets sank at once when I put them in water; others (apparently sound and germinable) I kept floating for a month. But I found a great quantity in February, floating in a lake at Kew, which must have been shed at the latest in the previous December, and I kept a

PLATE XII.



WATER-DISPERSAL. FLOATING FRUITS AND SEEDS.

FIG. 1.—*Oenanthe crocata* (fruit, enlarged).
„ 2.— „ „ (section of mericarp).
„ 3.—*Isoptera borneensis* (fruit).
„ 4.—*Sonchus palustris* (achene, enlarged).
„ 5.— „ „ (achene, in section).
„ 6.—*Orontium aquaticum* (seed, in section, enlarged).
„ 7.—*Lycopus europaeus* (nucule, enlarged).
„ 8.— „ „ (nucule, in section).
„ 9.—*Coix Lachryma-Jobi* (spikelet, fruit enlarged).
„ 10.—*Coix Lachryma-Jobi* (in section).
„ 11.—*Aglaodorum Griffithii* (fruit).
FIG. 12.—*Aglaodorum Griffithii* (fruit, in section).
„ 13.—*Thuarea sarmentosa* (inflorescence, enlarged).
„ 14.—*Thuarea sarmentosa* (single female flower).
„ 15.—*Thuarea sarmentosa* (single female flower in section).
„ 16.—*Philydrum lanuginosum* (seed, enlarged).
„ 17.—*Scutellaria galericulata* (nucule, enlarged).
„ 18.—*Caltha palustris* (seed, enlarged).
„ 19.— „ „ („ in section).
„ 20.—*Cyrtosperma lasioides* (seed, enlarged).

[*To face p.* 196.

number of these floating till March, when they sank (*see under Betula alba*, p. 227). I have certainly seen Birch trees growing on river banks that must have come from seeds which had drifted down the river.

Again, Guppy says that the nutlets of *Polygonum hydropiper* and *P. persicaria* are non-buoyant. This puzzled me, as I found plants of *P. hydropiper* on the Thames bank by the bridge at Kew, and it very quickly appeared on the embankment made the year previously, growing between the stones with other water-dispersed plants. The nutlets are lenticular, black and smooth, and I found that a considerable proportion of them floated for some weeks. *Polygonum persicaria*, also a common river-bank plant, occurs on the muddy banks of the river at Kew. It has similar nutlets, and they also float. Neither of these plants, so far as I can find, grow anywhere inland near the river-bank localities at Kew, and must have come a long way down the river to arrive at their present habitats.

LIST OF SEEDS AND FRUITS DISPERSED BY RIVER.

I give here some notes on the floating seeds or fruits which owe their dispersal in part or altogether to their buoyancy in stream and river, based mainly on the researches of Praeger, Guppy, and myself. Sea-dispersed plants are treated separately.

Some plants are here included whose fruits and seeds are floated down tidal rivers to the sea and are often stranded on the mud banks, forming tidal swamp plants, but which do not successfully cross the sea to distant coasts. The species are arranged in scientific order for convenience.

RANUNCULACEAE.

Clematis vitalba.—The achenes float for 12 hours (Praeger). They are regularly dispersed by the wind, and the plant does not usually grow near water. Its feeble floating power is adventitious or accidental.

Thalictrum alpinum floats for 2 days, *T. minus* 3 days, and *T. flavum* for 5 days (Praeger). *T. flavum* is a typical water-meadow plant, and grows also on river banks. It is certainly dispersed by river and flood.

T. alpinum is a mountain-stream plant, and probably is dispersed by stream freshets. *T. minus* is somewhat of a dry region plant. Wind probably plays the greater part in dispersing all these, but birds eat the achenes of the latter species.

Anemone nemorosa.—Achenes float for 1 day (Praeger). Possibly stream-dispersed in woods.

Ranunculus (*Batrachium* section).—The Water-Buttercups have very poor floating achenes, considering they are so common in damp pond edges and in rivers. At the same time it must be remembered that the larger number are submersed plants, and it is essential that their achenes should sink in the rivers. The river species, however, can be dispersed by floating portions of the stem. Praeger gives the buoyancy period of R. *trichophyllus*, R. *heterophyllus* and R. *Baudotii* as 12 hours only, and R. *Lenormandi* achenes as floating for 1½ days. The first three are submersed species, and are probably mainly dispersed by floating portions. The last is often to be found creeping in shallow pools on mud. It is certainly dispersed in some cases by the achenes adhering to the feet of cattle.

R. (*Batrachium*) *marinum*, of Denmark, Germany, etc., has intercellular spaces in the fruits (Ravn), which presumably float.

R. *sceleratus*.—This plant grows on muddy banks of streams, ditches and rivers, and is certainly dispersed by water. Guppy found its achenes floated from 1 to 4 weeks, Praeger for 3½ days only. Apparently there is great variability in the floating powers of the achenes. Guppy shows that the seeds germinate both in fresh and salt water. In the sea they took from April to October to germinate, in fresh water a few weeks only. Thus they may owe part of their migration to this method of dispersal. Ravn states that the carpels have an air-tissue system like that of *Alisma*.

R. *flammula*.—This grows on wet spots in low-lying marshy ground, but is not usually a river-bank plant. Praeger gives the flotation period of the achenes as 5 days, Guppy as 6 or 7 days. All those that I have experimented with sank at once.

R. *Lingua*.—The achenes float for 12 hours only, according to Praeger. Guppy says they are non-buoyant, and I have found that they sink immediately. The plant grows in marshes and ditches, and is probably dispersed by flood waters or violent stream spates, the achenes mixed with silt.

R. *ficaria*.—Praeger says the achenes float for 2½ days, Guppy for 6 to 7 days. The Celandine is, however, more readily water-dispersed by its leaf bulbils and subterranean bulbs, and, besides, the whole plant is often carried successfully down stream by rivers, as I have seen along the Thames.

R. *auricomus*.—The achenes are non-buoyant (Guppy). They float for 2 days (Praeger). Those of R. *bulbosus* float 3½ days, and R. *arvensis* 2½ days (Praeger). These Buttercups, being inland plants, possess but feeble and practically useless floating powers. The first species is a woodland plant, the second a pasture plant, and the third a cornfield weed, with adhesive achenes.

R. *repens*.—Praeger says the achenes float for 3½ days only, Guppy for from 6 to 12 months. This plant is common on tidal river banks and other muddy spots, and is abundant on the Thames bank at Kew. It is largely dispersed in this locality, however, by the drifting down of the whole plants as well as by its floating achenes.

Adonis annua.—The achenes float for 1 day (Praeger). This slight buoyancy is adventitious. The plant is a cornfield weed, and never likely to come into contact with running water.

Caltha palustris.—The fruit is follicular, and the seeds fall out on dehiscence. They float for from 1 to 4 weeks (Praeger and Guppy). The seeds are provided with a swollen persistent light raphe and chalaza, which form a floating organ. *C. radicans*, a stream plant, has seeds which float in the same way for 2 weeks (Praeger). (Pl. XII, figs. 18 and 19.)

Actaea spicata.—The berry floats for 1 week when fresh, and for 2½ months when dry (Praeger). This is probably mainly dispersed by birds, as it usually (at least in northern England) grows on dry limestone rocks.

DILLENIACEAE.

Dillenia indica.—This is a bushy tree, from about 20 to 60 feet tall, which grows almost always on banks of streams and rivers in India, Ceylon, and the Malay Peninsula and islands. The flowers are very large, and when the petals have fallen, the fleshy imbricating sepals close again, much enlarged and swollen, over the carpels, which are thin-walled and contain numerous small seeds. The sepals in fruit are ½ inch thick, and the whole fruit forms a round ball 6 inches through. It is sometimes eaten by elephants and the seeds passed, but usually falls into the stream or river, and is rolled and drifted away till it becomes stranded on a sand- or mud-bank. Here the sepals decay, or, as Troup says, termites eat them away, not touching the seeds, and fill the whole

ball with earth. Rain washes away the earth and the seeds germinate. The other species of *Dillenia* have similar but much smaller fruits, only adapted for dispersal by mammals or birds, and are not river-bank but forest or open-country plants. They are all very local species, and none have the wide distribution that this water-dispersed one has.

VIOLACEAE.

These are seldom, if ever, dispersed by water, except by rain-wash. In *Viola palustris* the seeds float for 2½ days, those of *V. canina* for 3 days, of *V. lutea* 1½ days, and of *V. hirta*, *V. Riviniana* and *V. arvensis*, 12 hours, and of *V. Curtisii* 18 hours (Praeger). The first is practically the only one, a marsh plant, which could thus be dispersed.

TAMARISCINEAE.

Tamarix.—According to Troup, the seeds of *T. gallica* (usually wind-dispersed) are also dispersed by water in India. Of *T. Troupii* and *T. dioica* he writes :—" On the banks of the Indus the newest alluvium thrown up by the " rain, and submerged by the annual floods for several years, until raised above " the surface of the successive layers of silt, becomes covered with multitudes " of Tamarisk seedlings of *T. Troupii* and *T. dioica*, which soon establish them- " selves in a dense crop of *Saccharum spontaneum*, the grass at last being killed " by the Tamarisks " (" Sylviculture "). The wind, however, as well as the water, has probably a good deal to do with covering these deposits both with the Tamarisks and the *Saccharum*.

BERBERIDACEAE.

Berberis vulgaris.—The dried fruit floats 1 hour, fresh fruits 4 days (Praeger). This is hardly ever likely to be water-dispersed, being an inland plant. It is chiefly dispersed by animals.

NYMPHEACEAE.

The *Nympheas* are submerged plants, with large round fruits which dehisce, and the separate carpels float for a short time. The seeds sink in all except *Barclaya*, as they require to germinate at the bottom of the water.

In *Nuphar lutea*, the common English yellow Water-lily, the fruit is globose, about 2 inches long, green, and usually raised to the surface of the water. It generally separates from the pedicel at the base, and the pericarp splits into 9 or 10 thin lobes from the base, halfway up, exposing 9 white masses, like the pigs of an orange. These are fleshy and contain about 16 round, smooth, rather soft seeds of a yellowish-brown colour. The pigs and fruit float as a whole ; the former are 1½ inch long. The seeds, when free of the pulp, sink. I placed some of the pigs containing seed in water on October 5th. By October 7th nearly all the pulp had melted away in the water, and nearly all the seeds sunk. By October 8th all the pulp had disappeared. In another experiment, on September 2nd, the next year, 3 days later 2 of the pigs were floating, the rest had dissolved and the seeds sunk. Thus the detached carpels can float for 2 or 3 days, and, should they go down a fairly fast flowing river, would travel for a considerable distance before the pulp was dissolved and the seeds sank. As a rule these plants grow in quiet waters, not running streams, but I have seen them often in ditches and pools, where they were almost certainly carried to by river flow.

Ducks and fish eat the pulp of these Water-lilies greedily, and, under the Dispersal of Plants by Fish, a case is given of a fish found to contain large numbers of uninjured Water-lily seed (*see* pp. 516 and 517). I threw a carpel of *N. lutea* into the tank at Kew, and immediately a large carp rose and chewed it, releasing it after a little while. It appeared to have sucked out the seeds and inner pulp. Tufted ducks and pochards bit and shook the carpels, but, apparently not being hungry, released them again. Evidence of ducks and heron swallowing the seed and passing them unharmed is given under accounts of those birds on pp. 489 and 494. Coots also, according to Clement Reid, swallow the seeds of Water-lilies. According to Praeger, the seeds of this plant (*N. lutea*) float when dry for 1½ weeks. These methods of dispersal seem to be the same for most of the genera *Nymphea* and *Nuphar*. They are also largely diffused by fragments of rhizomes being carried down rivers and into side branches under water.

According to E. P. Phillips (" Adaptations for the Dispersal of Fruits and Seeds," *South African Journ.*, ii, 240) the seeds of *Nymphea stellata*, which are hard and black, contain a small cavity filled with air, which makes them buoyant. This modification accounts for the very wide dispersal of this species, perhaps the most widely distributed in the genus. It is common in the Malay Peninsula, and very small forms of it occur in shallow ditches in Province Wellesley and other localities where ducks and such birds are completely absent, and unless the seeds float for a time, it is impossible to see how they could get into such spots.

The *Nympheas* are widely distributed all over Europe, Asia, Australia and America, but are absent from Polynesia and oceanic islands.

In *Nelumbium lotus* the fruits are enclosed in a much enlarged obconic, flat-topped, fibrous receptacle, shaped like the rose of a watering-can. They are embedded in holes in the top of the receptacle, which is very light when dry, and might readily be floated away. The plant is common all over Africa and India, but has long been cultivated for food and ornament in many places. I have never seen it spread in the Malay Peninsula further than it could by growth of the rhizomes, from some spot where it had been planted, but in India, according to Rangachari, the receptacles float away, and the seeds are so dispersed.

Brasenia peltata is a Water-lily of some interest, as it has rather a peculiar distribution. In Pliocene times it was evidently common in Russia, Germany and Switzerland, but has since quite disappeared from Europe. It is still found in Manchuria, North India, Japan, Australia, Angola and North America. The seeds are borne singly in separate fusiform carpels which do not dehisce, but fall separately and, I presume, float.

PAPAVERACEAE.

The seeds of nearly all the Poppies sink at once in water. They are, however, commonly disseminated by rain-wash.

Argemone mexicana var. *ochroleuca*, an introduced plant in Africa, is said by Mr. Burtt-Davy to have spread very rapidly down stream along the Vaal and some other rivers in South Africa. Miss Lansdell also records its dispersal by water in the same area. Maiden states that *A. mexicana* has spread similarly by water in New South Wales.

FUMARIACEAE.

Hardly any seeds of the Fumitories have any floating power at all. *Corydalis lutea* is recorded by Praeger to have seeds floating for 2 days, and *C. claviculata* for 12 hours. This latter plant I have seen in wet spots in the Norfolk Broads,

in localities where its seed might have been brought by water. Of *Fumaria Bastardi*, the seeds float for 12 hours, and those of *F. officinalis* for 8 hours; but no species of *Fumaria*, and but few of *Corydalis*, grow in spots where they are likely to come into contact with running water.

HYPERICINEAE.

Hypericum elatum and *quadrangulum*.—Of these the seeds float for 1 day, those of *H. calycinum* and *H. elodes* 12 hours only (Praeger). The latter is a marsh plant, and is probably dispersed by attachment to the feet of marsh birds. The seeds of these plants are very small and light, and dispersed largely by wind.

MALVACEAE.

Praeger gives 2½ days for the buoyancy period of seeds of *Malva moschata*, 1½ days for *M. sylvestris* and *Lavatera arborea*, and 12 hours for *Malva rotundifolia*. The seeds of *Hibiscus* do not, as a rule, float, except those of *H. tiliaceus*, *H. Youngianus*, of Hawaii, *H. diversifolius*, and *H. Abelmoschus*. The first-named is a sea-dispersed species, but is also distributed up tidal rivers. The others are not sea-dispersed plants, nor do they appear to be, often at least, water-dispersed. *Paritium tiliaceum* is sea-dispersed.

FLACOURTIACEAE.

Trees or shrubs usually with baccate fruits, the smaller ones bird-dispersed.

Pangium edule, a large Malayan tree with big oblong fruits 1 foot long, containing a number of seeds in an oily pulp. The seeds are about 1½ inch long, with a fibrous woody hard shell, subtriangular. The tree frequently grows on river banks, and the seeds float easily for a long time. They are often to be found in Malayan sea-drift, but do not survive the action of sea-water. I have found them drifted up on the shores of Christmas Island, and Ross gave me some from Cocos-Keeling Islands, where Guppy also got them. Schimper records them as sea-drift in Java also. The seeds never seem to have reached any oceanic island alive.

Hydnocarpus venenata.—This is a river-bank tree with globular fruits about 1 inch in diameter, containing usually 6-angled seeds which are poisonous to fish. Lewis (*Ann. Bot. Gard.*, *Peradeniya*) says the fruit is water-dispersed in Ceylon.

CRUCIFERAE.

Very few of this large order are waterside fruits, and very few have floating seeds or fruits.

Matthiola incana, a sea-cliff plant. The seeds float for 2 days (Praeger).

Nasturtium officinale, the Watercress. The seeds float, according to Praeger, for 12 hours only. Guppy says they do not float at all. There is no doubt, however, that the plant does get about by water. In the tidal mud at Kew there is a curious little submerged dwarf form, but I do not know of any typical plants of the species within many miles. It possibly travels by the transport of fragments of the stem, as it readily grows from pieces. I have found it growing on stumps of trees above water in the River Kennet, near Reading, which it must have reached by drifting in a rise of the river.

N. palustre.—The seeds float for about 12 days (Praeger). This is undoubtedly river-dispersed. I find it in many spots by the river at Kew, where its seeds can only have been carried by water, on walls at high-tide marks, etc. After the heavy floods of 1927 on the Thames, I found a plant or

two growing in Meyer's Passage, near Kew Green, 120 yards inland from the river bank (1928), the seeds having evidently been carried up during the high floods and deposited on the roadside. Seeds put in water October 30th (1929) floated till November 3rd.

Cakile maritima and *Crambe maritima* are sea-disseminated plants, and their history is given under that heading. *See* p. 259.

Raphanus raphanistrum.—The fruits of the radish float (according to Praeger) for 5 days, those of the sea-coast R. *maritimus* from 3 to 4 weeks (Guppy and Praeger). These float by the corky pericarp, for the seeds are not buoyant. The joints of the pod are separated by a narrow neck and break off readily. There are 1 to 4 joints to a pod. Guppy records finding pods of a species allied to R. *maritimus* in the strand-drifted debris of beaches in Southern Chile, which floated from 7 to 10 days after 6 weeks' drying. There does not appear to be any indigenous species of *Raphanus* in Chile, and these were probably the pods of the cultivated radish.

CAPPARIDACEAE.

Crataeva religiosa.—This Asiatic shrub has a hard, round, many-seeded berry, rather dry. It grows in India by streams among boulders, and is apparently water-dispersed (Troup). *C. macrocarpa*, of Malaya, Burma, and Indo-China, is also a river-bank plant, a tree with hard, oblong-globose, woody fruits, 2 or 3 inches in diameter, which is probably also dispersed by the river-currents.

CARYOPHYLLACEAE.

Stellaria aquatica, a river-bank plant.—Some seeds floated from September 22nd to 28th. After sinking, they germinated in 4 days and floated again.

GUTTIFERAE.

Calophyllum macrocarpum, of the Malay Peninsula, is a river-bank tree with large, corky, brown 1-seeded fruits, which are certainly water-dispersed. *C. inophyllum* and *C. calaba* are sea-dispersed.

Kayea stylosa, a large tree with fruits enclosed in the woody accrescent sepals, seeds 1 to 4, a native of Ceylon, is stated by Lewis to be water-dispersed. Several species of the genus in the Malay Peninsula grow by the edges of forest streams, and I have very little doubt that their corky sepals are an adaptation for water-dispersal.

Mesua ferrea.—In most of its area—India, Ceylon, and the Malay Peninsula—this tree is found in forests away from water. Mr. Kanjilal notes that in Sibsagor, in India, natural reproduction takes place freely in swampy localities under the shade of *Dillenias* and Laurels, the seeds being deposited by water (Troup).

DIPTEROCARPACEAE.

These are big Indo-Malayan trees, of which the larger number have winged fruits dispersed by wind, but some of these also float readily in water, owing mainly to the lightness of their wings, and where they grow on the banks of forest streams or rivers, they are transported both up and down stream by water. One of these is *Dipterocarpus oblongifolius*, which grows on the sloping hill-sides of the River Tahan in Pahang, Malay Peninsula, and by other rivers on the east coast. I have seen the fruits floating in the river, with the two sepaline wings projecting partly above the water, so that the wind blew them upstream against a strong current. Many drifted ashore to both banks, some distance from where they had started. Off the east coast I saw fruits of this tree floating in the sea from the Tringganu River, but all these fruits were rotten.

Isoptera borneensis is a tree of no great size, usually about 40 feet tall. In the fruits of this plant the 5 sepals are spread out so as to form a kind of round plate. They are rounded, rather thick, corky-woody, and stiff. The ovary is a globose body in the centre. The whole plate of sepals is about 1 inch or more across. These fruits float very readily and are borne about the streams and rivers in the forests of the Malay Peninsula and Borneo (Pl. XII, fig. 3).

In *Pachynocarpus* (included under *Vatica* by van Slooten) the sepals in fruit are usually reduced to short corky lobes. Occasionally they enclose the nut in the form of a thick corky coat (*P. umbonatus*, *P. Stapfianus*). Where (in the *Vateria* section) the sepals are reduced to small corky lobes, the walls of the ovary become corky and thick. The greater number of these trees grow in the lowland swampy districts of the Malay Peninsula, or by streams. Van Slooten writes :—" They occur in primeval as well as secondary forests, " in level as well as in hilly localities. Nearly always they prefer a humid or " wet soil, which either may be inundated during a high tide or only during " the west monsoon. Swampy forests and river banks are for *Vatica* (*Pachyno-* " *carpus*) very common habitats. Sometimes they have been found on or near " the beach." Of *P. Wallichii*, Foxworthy says : " Its natural habitat is upon " ground liable to flooding. The fruit is dry and water-dispersed, usually by " means of floods." I have found it on stream banks. Of *P. papuanus* (*Retinodendron papuanum*) the large fruits have been found by Moseley (Hemsley, Challenger Reports) off the Aru Islands, floating on the sea-beach. *P.* (*Retinodendron*) *Ridleyanus* does not grow in swamps. It has a long, subconical corky fruit. It grows in dry woods in the Malay forests. The fruit sinks in water. This fruit is therefore not water-dispersed, but is probably carried about by rats or ground-squirrels, to feed on the corky outside, much as the fruits of *Scirpodendron* are.

The fruits of *Vateria* and *Stemonoporus* in Ceylon (which are somewhat similar to those of *Pachynocarpus*) are water-dispersed, according to Lewis, and Trimen says that the *Vaterias* grow by streams. Though *Pachynocarpus papuanus* has been found drifted to the Aru beaches, it seems that these fruits, though they must often reach the sea in river-drift, never succeed in establishing themselves on distant islands. Their modification for water-dispersal merely serves to spread them in the low wet forests which fringe the coasts of the larger islands and mainland of the Malay Peninsula. These wet, constantly inundated tracts of forest are of very large extent in the Malay Peninsula on the west coast, often 36 miles wide and running for the greater part of the Peninsula from north to south. In many parts of Borneo, Sumatra and the Malay Peninsula the larger rivers running down from the interior are fringed for a long way with water-woods, where the river flows through dense forest on either side of its main channel. In these almost impenetrable woods the water lies at various depths, and may increase with a rise of the river, and it is in such places that these water-dispersed plants are found.

STERCULIACEAE.

The sea-dispersed and tidal river *Heritiera* is described under Sea-Dispersal, as is also the river-bank and littoral *Kleinhovia hospita*, with its bladder-like fruits, which are dispersed both by wind, river and sea. *See* pp. 73, 262 and 263.

HUMIRIACEAE.

Saccoglottis amazonica is a small tree of the Amazon River. The fruit is an oblong drupe of which the stone is light, normally 5-celled, with 2 cells usually suppressed. It contains numerous closed cavities or resin-cysts. These fruits,

deprived of their outer skin, float easily for many months, but probably lose their germinating power in 6 months. Neither the substance of the drupe nor its seeds are buoyant; the buoyancy is due to the numerous round empty cavities in the fruit. It is widely distributed by sea, dead drupes being found on the coasts of Azores and the British Isles; but though the tree occurs as a rarity in Trinidad, it is found in no other West Indian island, nor has it reached Africa. The tree is found far up the Amazon River. I exclude this from sea-dispersed plants as it has failed entirely to cross the sea and establish itself anywhere except in Trinidad.

BALSAMINACEAE.

Impatiens.—The fruits of these herbs are explosive, and the seeds are dispersed only in this way in many species, but some at least have buoyant seeds which, when thrown into the water from the river banks on which they grow, are carried along by the current. Species like *I. Wrayi* and *I. sarcantha*, in Perak, Malay Peninsula, which habitually grow on rocks in the streams, can only reach these positions by the floating of the seeds. Of *I. polycycla* I found a single plant in a sand-bank in the Kertai River, Perak, and though I searched for it a long way up and down stream, I could not find another plant. The seed must have been drifted down from a long distance up stream. *I. fulva* is a native of North America, and was introduced into England in 1822. It inhabits river banks. The capsule on exploding throws some of the seeds into the water, or on to the edges of the banks, where, by a rise of the tide or flood-water, they are washed away and float down stream till they are stranded and grow. It is now very abundant in several parts of the banks of the Thames, the Wey, Tillingbourne, the Mole, and Basingstoke Canal. It is plentiful between Richmond and Kew, and has comparatively recently spread down river as far as Barnes in spots where its seeds can only have been transported by water and thrown up by high tides and floods.

Hydrocera.—The Water-Balsam of the tropical Asiatic region, which has an indehiscent berry of 5 carpels, each containing a single seed, is almost certainly water-dispersed. It is found in marshes and rice-fields.

RUTACEAE.

Citrus.—"Other instances of the useless buoyancy of fruits of inland plants "are afforded by different species of *Citrus*," says Guppy; but though these fruits soon perish at sea, and are quite unable to effect a lodging on a distant seashore, the floating power of such inland plants is not really wasted. Like many other riparian plants, they can spread down rivers, perhaps be transferred by floods to other rivers, and so spread over the country. In the floating drift of the Fijian rivers Guppy says the fruits of the wild and indigenous Shaddock (*Citrus decumana*), and of an inedible orange, also wild and indigenous (*C. vulgaris* ?), are at certain times to be found, and often in numbers. The Shaddock (i.e., Grape Fruit) floats 4 to 5 weeks in sea-water, and the wild orange nearly 2 months, and both are to be observed floating out at sea between the islands. The fruits of the Tahitian Orange—a variety of *C. aurantium*—float in sea-water between 3 and 4 weeks. Their buoyancy is due to the rind, as the seeds sink. Seeman records the occurrence of the Shaddock in Fiji along the river banks, which it thickly lines. The fruit of *Merrillia caloxylon*, which has a very thick rind, is probably to some extent river-dispersed, as the tree is abundant where it occurs on the river banks of the Malay Peninsula.

ILICINEAE.

Ilex aquifolium.—Praeger states he has found that fresh Holly berries will float 2 days, and dry seeds 1½ weeks. I find both sink at once. The seeds are dispersed by rain-wash after being passed by birds, but I doubt if they are ever dispersed by streams or rivers. I have never seen a Holly plant in any position suggesting it has been brought by water, but I have seen Holly seeds drifting about on ice, where they had been evacuated by blackbirds.

CELASTRINEAE.

Euonymus europaeus—The dry fruit floats for 2 months, seed 2½ days (Praeger). This is also a bird-dispersed plant of an inland habitat.

RHAMNACEAE.

Rhamnus catharticus and R. *frangula* have drupaceous fruits dispersed by birds. Praeger says that the dry fruit of R. *catharticus* floats for 6 days, and the seeds for 3½ days, and the fresh fruit of R. *frangula* for 2 weeks and 5 days, and the dry seed for 1 week. Neither grow near water, and it is unlikely that this buoyancy is of any importance to the plants.

SAPINDACEAE.

Melianthus major, a herb, native of South Africa, introduced as an ornamental plant in New Zealand, has very light papery capsules, dehiscing at the tip. E. H. Atkinson (in "Weeds and their Identification," *New Zealand Journal of Agriculture*, 1922), says that in New Zealand it spreads along river banks, and the seeds are doubtless carried by water in their inflated capsules. (*See also under* Bladder Fruits, p. 73.) The dispersal of *Dodonaea viscosa* and *Cardiospermum halicacabum*, which also have dilated papery capsules, is dealt with on p. 73. Both are disseminated by wind and sea. *Staphylea* (*Staphyleaceae*), a genus of European plants with bladdery pods, is probably dispersed by water as well as by wind, but I have no evidence of this.

ANACARDIACEAE.

Gluta Benghas.—This tree has corky fruits, 1-seeded, 1½ to 2 inches through, which certainly can float, and it is an inhabitant of river banks. It is reported to have reached Krakatau. *G. coarctata*, a tidal river plant, whose brown corky fruits may be seen abundantly floating about in tidal rivers, is described under Sea-Dispersed Plants, on p. 270.

Most of the other *Anacardiaceae* are dispersed by birds, a few are modified for wind-dispersal.

LEGUMINOSAE.

A good many of the plants of this order have floating pods or seeds, and a number of species are sea-dispersed, both by buoyant pods, *Derris*, *Dalbergia Cassia*, *Pongamia*, and by floating seeds, *Mucuna*, *Entada*, etc. These are all treated of in Sea-Dispersed Plants on pp. 271 to 287.

J. Buchwald, in a paper on the dispersal of *Leguminosae* of Africa, gives a long list of species which he says have fruits or seeds adapted for floating. He does not, however, state that he has seen them floating, nor does he give

any account of their buoyancy. Of some of them, e.g., *Abrus precatorius*, the *Tephrosias*, the seeds are distinctly stated by Guppy to be non-buoyant. Others are dealt with under Sea-Dispersal, and others, again, are inland plants which can very rarely, if ever, come into contact with stream or river, though their seeds or pods may be dispersed by rain-wash. Such are *Stylosanthes mucronata*, *Desmodium polycarpum*, *D. triflorum*, *Alysicarpus nummularifolius*, and some *Crotalarias*. These plants mostly grow in pastures or dry open spots. In *Crotalaria* the often inflated pod dehisces and drops the seed out when ripe. Some, however, that Buchwald mentions are riparian or wet-ground plants, and are almost certainly disseminated by water. Such are *Aeschynomene indica* and *asperata*, *Herminiera*, *Neptunia oleracea*, in all of which the joints of the pods, or the whole pod, may float. He states also that *Vigna nilotica* and *abyssinica*, *Rhynchosia minima*, *Teramnus labialis* and *Tephrosia Vogeli*, and other species, have seeds with spongy cotyledons, by which they float. Further information, however, on these plants is required.

Certainly the greater number of the seeds of leguminous plants, and especially of the *Papilionaceae*, do not float at all. Praeger and Guppy have tried most of the British species, and have shown their non-buoyancy. A few have pods which float for a short time, but these are usually inland plants which would hardly ever be likely to derive any benefit from this buoyancy.

Lathyrus palustris is a climbing marsh, fen or river-bank herb, of which the seeds float readily in water. It is found in England and Ireland, as well as in many other parts of Europe, and is especially abundant in Siberia along the Amur and Ussuri river banks, and is also found along streams in China and Japan. The seeds are small and globose, with a thin, rather soft testa. The cotyledons float readily when freed from the testa, and it is evidently from their light texture that the seed floats. In section I see no air-space in the seed. The same appears to be the case in *L. maritimus*, which I treat of under Sea-Dispersed Plants, p. 271, though in this the raphe seems to consist of looser cells, which might aid in its floating. Still, the buoyancy of the cotyledons is quite enough to account for this.

I have experimented with the seeds of a number of other species, and Praeger has done the same with *L. pratensis*, *L. latifolius*, *L. sylvestris*, *L. montanus* and *L. niger*, and in all these the seeds sink at once. They are all inland plants. In those I have examined, e.g., *L. tingitanus*, the cotyledons, deprived of the testa, sink like stones, though in texture they do not appear to differ from those of *L. palustris* and *L. maritimus*.

Praeger records that the seeds of *Anthyllis vulneraria* (perhaps in the inflated pod) float for 1 day, and those of *Onobrychis sativa* for 5½ days, but neither of these plants lives in damp spots or near water, and their buoyancy is more of an accident. The pods of *Anthyllis* are dispersed by wind, and many wind-dispersed fruits can float a short time in water.

No other of the British herbaceous *Leguminosae* seem to have floating seeds, though the fruits of most of the *Medicagos*—*M. lupulina*, *M. arabica* (*maculata*), *M. denticulata*, *M. minima*, and of *Trifolium arvense*, are reported to float from 1½ to 5 days. Guppy states that the pods of the *Medicagos* figure largely in beach-drifts. The pods of several kinds form a feature in the Sicilian drift, and he observed the pods of a small hairy species growing on the beach at Taormina, whose seeds were germinating in the sea-drift, and he has seen also fruits of *Medicago* in the Chilian beach-drift. However, it does not appear that any of these plants are dispersed by water, except as seedlings, as I show in *M. lupulina*, p. 188, as they are not to be found growing in damp spots or on river banks.

Sutherlandia frutescens is a leguminous shrub with thin-walled bladdery pods. It is about a foot or so tall, and is a native of Southern Africa. The pods become readily detached and do not dehisce. I have seen them blown along

the grass at Kew for a few feet. Mr. Burtt-Davy writes me: "It is a native "of South Africa, but, owing to its wide distribution along streams, I feel "uncertain as to the precise part of Africa which is its original home. It "occurs in the Transvaal, but I am inclined to think it is a Cape Karoo species."

Colutea.—This is also a genus of *Leguminosae,* with thin-walled bladdery pods. *C. arborescens,* of India, and *C. aleppica* grow on shifting sands and in deserts, and are doubtless dispersed by wind (*see* section on Wind-Dispersal, p. 73). *C. salsola* and *C. Delavayi,* of China, are said to grow on sandy banks of rivers and in the hedges by streams. These are undoubtedly river-dispersed.

Dalbergia Sissoo is an Indian tree with thin, flat light pods containing 1 or 2 seeds, which are dispersed over the flood plains of India by water as well as by wind. It grows on alluvial flats and river banks (Troup).

D. torta (*D. monosperma*) is more of a tidal swamp plant, climbing on bushes. Its pods were seen by Guppy floating in the estuary of the Rewa River in Fiji, but it is largely sea-dispersed, so I treat it under that section, p. 276.

Cassia.—The cylindrical, many-seeded pods of the section *Fistula* float, and are to some extent river-dispersed. An account of those of *C. fistula* is given under Sea-Dispersal, on p. 279. *C. nodosa,* with similar pods, is abundant on the edges of the Malay rivers, and seems to be river-dispersed, as are probably the thick pods of *C. braziliensis* in South America. These pods do not dehisce on the tree. *C. siamea* is an inhabitant of the river banks of the Malay Peninsula. Its pod dehisces on the tree, and it is possible that its seeds float, as the plant managed to reach Krakatau after the eruption.

Crudya spicata, a big South American tree, of which Guppy found the fruits and seeds floating in the river-drift of Jamaica, the seeds in a germinating condition. They were not in a suitable state for crossing the sea to Africa, and he was puzzled at the distribution of the genus, which contained 13 American, 1 Philippine and 1 African species. Since he wrote, however, no fewer than 10 species have been found in the Malay Peninsula, 1 or 2 in Siam, and 1 in Ceylon, showing the genus to have a pan-tropical distribution. All the Asiatic species are curiously local and scarce, suggesting a considerable antiquity for the genus. The Malayan species at least are not inhabitants of river banks, occurring in forests and rather dry spots, but doubtless the Jamaican one is dispersed by river water.

Acacia.—These trees have thin pods, usually flat, with several seeds. Many are dispersed by wind, and by cattle and other animals eating the pods and passing the seeds. *A. arabica* comes up with Tamarisks on alluvial flats, where its pods are carried by water, and the same thing occurs in *A. catechu* and *A. eburnea,* in India (Troup). *A. Farnesiana* is also distributed along rivers (Troup). The pods in this species are thick and pithy, quite light when dry. An account of it is given under Sea-Dispersal, p. 286.

A. laurifolia, a coast plant on the Fijian beaches and in other Pacific islands, has pods which break up into joints, each containing a seed. These float for a week or two. Guppy thinks that its distribution among the islands may be due to water-dispersal.

Inga (*Samanea*) *Saman.*—Seeds in good condition were found floated up on the shores of Volcano Island, in Lake Bombon in the Philippines, by Merrill (*see* "Island Floras," p. 679). It, however, does not owe much, if any, of its dispersal in its native country, South America, to water action. It is really an inland plant, the seeds of which are dispersed by ungulate mammalia feeding on the pods.

Aeschynomene indica and *A. asperata,* now very widely distributed in the world, are marsh and river-bank plants, with pods of corky joints, which separate and are very light, and no doubt buoyant. *Herminiera,* an allied plant, has similar curled hairy pods, breaking up into points, and similarly corky.

This is abundant in African rivers. *Aeschynomene* is pan-tropical, but absent from oceanic islands. *Ae. indica* is very widely distributed in Asia to Papua, and was in Australia in 1802. Possibly the small segments are attached to the feet of birds in mud. It is certainly, however, associated with rice culture. Both of these genera are undoubtedly water-dispersed by their seeds as well as by the floating stems in the big African and Indian rivers. *Sesbania*, a genus of similar habit and habitat, has long, slender, many-seeded dehiscent pods with small oblong seeds which sink in water immediately. Their wide dispersal is doubtless due to their being accidentally mixed with rice grains.

ROSACEAE.

Spiraea ulmifolia (the Meadow-sweet).—The small 1-seeded carpels float in rivers (according to Guppy) for 3 weeks. They did not, he says, float longer when he increased the density of the water, but the number that floated for a given time was larger. Praeger gives their floatation period as 1½ weeks. The plant is common by watercourses, and I have found it along the Thames bank as far down as Kew Bridge, evidently brought by river.

S. filipendula.—The carpels of this chalk-down plant float for 1½ days only (Praeger). It is unlikely from its habitat to be ever dispersed by stream.

Sanguisorba officinalis, according to Praeger, only floats for 2 days. Holmboe (in "Studies of the Vegetation of Cyprus") records the floating down stream of the fruits of *S. spinosa*.

Of the other English herbaceous *Rosaceae*—*Agrimonia*, *Alchemilla*, *Potentilla*, *Geum*, *Dryas*, *Poterium*—none, according to Praeger, have seeds which float for more than 2½ days, except *Agrimonia Eupatoria*, 1 week, and *Potentilla anserina*, which floats 15 months. This latter common roadside plant also occurs on the Thames river bank by Kew Bridge and at Mortlake, where it undoubtedly appears to have been drifted by the river.

The aquatic *Comarum palustre*, however, has carpels which will float for from 12 to 15 months or more. The carpels, which are very minute, are borne on a spongy conic receptacle which is, I believe, eaten by ducks and other water-birds.

Of the woody British *Rosaceae*, the fresh fruit of *Rosa spinosissima* and the dry fruit of R. *arvensis* are reported by Praeger to float for 1½ months, dry fruit of *Pyrus Aucuparia* 2 weeks, and fruits of *Crataegus oxyacantha* from 2 to 4 weeks. All these are mainly dispersed by birds, but I have seen the *Crataegus* (Hawthorn) berries floating in the river, and I have seen trees or young plants in positions on the river banks, far from other trees, which certainly suggest their having been brought down by stream. The seeds sink, it is the pithy pericarp by which the fruits float.

Parinarium laurinum, in Fiji, is found floating in estuaries, and also occurs in the Solomon Islands. The fruit is hard and resinous, 1½ inch long. This owes its buoyancy to the light outside layers of the fruit. It floats for months (Guppy). *P. insulare*, the Sea-tree of Fiji, has large fruits with 2 cells, one containing a hairy seed, the other hair only. It is said to be dispersed by fruit-pigeons. All the fruits found floating by Guppy were empty. It is peculiar to Fiji.

SAXIFRAGACEAE.

The seeds of *Saxifraga* are all non-buoyant so far as is known. Those of *S. stellaris*, recorded by Praeger to float for 1 day only, and those of *S. aizoides* and probably other mountain species, are dispersed by stream-currents. The seeds of *S. aizoides* are recorded by Praeger as non-buoyant.

Parnassia palustris.—The seeds of this plant float for $3\frac{1}{2}$ weeks (Praeger). The seeds are very light, and most probably mainly dispersed by wind.

Adoxa moschatellina.—The seeds float, according to Sturm. This plant usually grows in woodlands, though also by streams. The fruit is a berry, and the peduncle bends downwards when the fruit is ripe, and it is quite possible for seeds to get into a stream and so be dispersed.

Platylophus trifoliatus.—Phillips states that the capsules of this plant of South Africa are dispersed by streams and flowing rivers. They are small 2-celled capsules with 2 ovules in each cell, only 1 in each developing into a seed. I have no records of any other plants of this order whose seeds are dispersed by water.

DROSERACEAE.

Drosera.—The seeds of the Sundews float for various periods, those of *D. rotundifolia* from 3 to 4 weeks, of *D. longifolia* 1 month, and *D. anglica* $5\frac{1}{2}$ days. These plants always live in damp spots, among *Sphagnum*, or on the bare ground, and not in positions in which they are likely to be spread by streams or rivers. Indeed, they grow in the same class of ground in which *Pinguicula* grows, the seeds of which hardly float. Still, the species are much more widely spread than are those of that genus. It is possible that in low-lying districts floods or rushes of rain-water may play some part in their distribution.

HALORAGACEAE.

Myriophyllum verticillatum.—The seeds of this aquatic float for 1 day only (Praeger). It is probable that it is mainly dispersed by detached portions of stems. (*See under* Dispersal by Vegetative Organs, p. 184.)

Hippuris vulgaris.—In this aquatic plant the fruiting stems fall over in the water, and the minute 1-seeded fruits drift away and eventually sink. According to Praeger, they float for over 15 months.

Callitriche.—In all the species examined the minute fruits sink. These aquatic herbs are dispersed, mainly at least, by floating fragments, but also doubtless by birds, either by attachment of the seeds, or, rather, fruits, to their feet, or by attachment of the fragments of the plant to water-birds. The distribution of the smaller tufted species, e.g., *C. stagnalis*, is probably effected by the rolling of the fruits along the shallow waters of tidal mud. They are all submersed plants, so that the drifting of floating seeds would strand them above the water, where they could not grow. Hence buoyancy of the seeds would be a disadvantage.

Gunnera magellanica.—The *Gunneras* have small, more or less pink succulent berries, which, though not very conspicuous, are probably dispersed by birds. S. Birger ("Du Vegetation bei Port Stanley, Falkland Isles," *Engler's Jahrbuch*, 39, p. 303) states that out of 100 seeds of *G. magellanica*, 2 floated for 5 days.

MYRTACEAE.

Eugenia.—The Tree Myrtles are a vast genus very widely spread, and this is undoubtedly due to their dispersal by birds and fox-bats, but some of the river-bank and seashore species may also be dispersed short distances by water. Guppy made some experiments on the Polynesian species *Eugenia corynocarpa*, *E. rariflora*, *E. Richei* and *E. rivularis*. The ripe fruits sank in sea-water in from 7 to 10 days; those of the Beach Tree, *E. Richei*, floated a fortnight, the decay of the fleshy pericarp causing them to sink. He noticed that fishes bit the pericarp as they floated. The seeds all sank at once, except in one species, in which the seed loosely filled the testa, and it floated for a few days. It is

quite possible that the fruits might cross a tract of sea from 200 to 300 miles wide. *E. salictoides*, of the Tahan River, Pahang, is a regular river-bank species, with white pithy fruit ½ inch through. It is so abundant on the river edge and islands that I have little doubt it owes most of its distribution along the banks by the wash-down of the fruits. Undoubtedly many seeds of *Eugenia* are rolled about the forests of the Malay Peninsula by rain-wash and shallow streams, but the genus is, as a whole, bird- and bat-borne.

Grias cauliflora.—The Anchovy Pear Tree is a native of South America and the West Indies. It has a large elliptic drupe 3 to 3½ inches long, with a woody pericarp (with 8 prominent ribs), which is buoyant, the seed itself sinking in water. Guppy gives a good account of its habits in "Plants, Seeds and Currents," p. 211. Its fruits float readily in rivers along the banks on which it grows. At the Roaring River Falls, in Jamaica, it grows not only on the brink of the falls, but in the wash below them, as well as halfway down their face, where the fruits have caught in the crevices of the calcareous tufa. The fruits readily get into the floating drift of rivers and can float for months, and germinate in the river-drifts. They are, however, destroyed by the sea, though the stones may be found drifted up on beaches.

Barringtonia spicata, *B. acutangula*, etc.—These plants, with their long pendent racemes and oblong fruits, are the inhabitants of river banks, and are certainly river-dispersed. The seed is enclosed in a light pithy pericarp which readily floats. Several of the other species are tidal mud and littoral plants which are sea-dispersed. The thick, fleshy, corky pericarp (calyx-tube) is clearly the floating apparatus.

MELASTOMACEAE.

Ochthocharis is a river-mud or forest-swamp genus in which the berries are not succulent and bird-eaten, as is the case in many species of the order, but quite dry, irregularly dehiscent, with corky seeds, is certainly water-dispersed. They are natives of wet Malayan forests. There are about 8 species.

Perilimnastes fruticosa.—This plant forms compact tussocks in cracks of rocks in mountain streams on Gunong Tahan, Pahang, in the Malay Peninsula. The capsule resembles that of *Sonerila*, and dehisces by 4 valves at the top. The seeds are flat and light. As the plant is quite confined to rocks in the centre of the rapidly rushing streams, it is impossible for it to be disseminated except by the rush of water.

RHIZOPHORACEAE.

These are chiefly sea-dispersed plants, and specially modified for that purpose. They are treated of under that heading, p. 287.

COMBRETACEAE.

Terminalia.—The flat-fruited species, *T. foetidissima*, etc., and those with 4-angled fruits, like *T. arjuna*, are certainly to some extent river-dispersed. *T. Catappa*, which has flat round fruits like those of *T. foetidissima*, is adapted for a seashore life and a sea-dispersal. *See* p. 290.

Combretum.—The 4-angled fruits of the section characterised by *C. trifoliatum* are certainly river-dispersed. The plants grow on river banks, climbing over shrubs and trees. I have found the fruits of *C. tetralophum* floating in the sea in Singapore. They must have been brought down by river. These plants are about 1 inch long, and are 4-angled; the pericarp and calyx-tube are thick

and woody, protecting the seed from the action of water. It is a riparian climber.

Quisqualis also has floating fruits and occurs on river banks, but as it has also migrated by sea to a considerable distance, it is treated of under that heading (*see* p. 290). This class of river-bank plant which can be sea-dispersed must owe much of its continental distribution to river and flood action.

LYTHRACEAE.

Lagerstroemia tomentosa.—Troup notes the prevalence of these trees in India by natural reproduction round the edges of swamps and water-courses. *L. floribunda* and *L. ovalifolia* are certainly riparian plants in Pahang, on the east side of the Malay Peninsula. The very light seeds of the *Lagerstroemias* are naturally wind-dispersed, but I think in many cases where they grow on river banks, water is an additional factor in their distribution.

Lythrum salicaria is at first a puzzling plant, as it is truly riparian, and may be seen gradually making its way along river banks, yet its seeds are not buoyant, but sink immediately. However, I find that they germinate under water after a few days, float to the surface, and are dispersed as seedlings. *Peplis portula* has also non-buoyant seeds, and is perhaps dispersed by attachment of the seeds to birds' feet.

ONAGRACEAE.

The seeds of most of the *Epilobiums* float for a day only, and *E. palustris* at least, only with the hair-plume attached, the seeds sinking when this is removed. The buoyancy is probably due to an air-bubble entangled in the hairs.

Oenothera biennis.—Some seeds floated, when I put them into water, for a short time, but I am not certain these were not barren ones. *Oenothera odorata* seeds float only 1 day (Praeger), as do the fruits of *Circaea lutetiana*, but I doubt if any of these plants owe their distribution to any water action except rain-wash.

Jussiaea.—These herbs with very small seeds take the place of *Epilobium* in the tropics, but as the seeds are not plumed, they are not so abundant. Guppy says that the seeds of *J. villosa*, of Hawaii, float for a few days. I think probable that water plays some part in the dissemination of these plants, from the positions in which they occur. Evidence, however, is required as to how far any can be floated.

Trapa natans and *T. bispinosa.*—These floating plants are mainly dispersed whole by river and flood. The fruits are mentioned by Grant as drifted upon the shores of the African lakes, and according to many authors they float readily. They are large and obconic, with stout processes, the whole resembling the rough outline of a bull's head and horns, and are hard and black, about $1\frac{1}{2}$ inches across. *T. natans* is found from Europe to China and Japan, Kashmir and Africa, *T. bispinosa* in India, Tonkin and Africa.

T. natans formerly occurred in Norfolk and Suffolk in pre-glacial times, but has long disappeared. The plant is cultivated by Chinese and other natives for the fruit—Water Chestnuts—but was evidently at one time very widely spread naturally over the whole European, Asiatic and African areas.

CUCURBITACEAE.

Hodgsonia capniocarpa.—A large climbing Gourd on river banks in the Malay Peninsula and Sumatra. The plant is not to be found in tidal rivers, but a long way up above the tides. The fruit is very curious. It is round, flattened

at both ends, 6 inches across, and covered with a short smoky-grey tomentum. The pericarp is woody, and it contains a number of large angled seeds 2 inches long, embedded in an oily pulp, not unlike those of *Pangium edule*. The fruit floats easily when it falls into the water, and, owing to the fine velvety plush which covers it, can be taken out as dry as when it fell in. The seeds float as well, and I have received them from Cocos-Keeling Island collected among drift seeds. As it seems to be an up-river plant only, it has failed to establish a footing on the more distant islands.

Fevillea cordifolia is another large-seeded Pumpkin, from South America, of which the seeds appear in sea-drift, but which has not apparently spread except by river.

The seeds of some other *Cucurbitaceae* float for short periods—*Bryonia dioica* 3 days (Praeger), those of *Cucumis acidus* and *Cucurbita* sp. some months (Guppy). He mentions these as found in river-drift in Chile. He also mentions the floating of small bottle Gourds in the Fijian estuaries and in the sea off the coasts. These are more or less globular, 3 or 4 inches across, and are evidently able to float for a long time and carry the seeds unharmed. Those from the drift he found were dry inside, and contained the seeds dried into a loose ball about 1 inch in size. The seeds were non-buoyant. One fruit floated in sea-water for 2 months, and after being kept for 7 months it was broken open, and of the seeds 2 germinated in 2 days when planted. Somewhat similar Gourds were picked up floating in the Guayaquil River, Ecuador. They were, however, specifically distinct, and the seeds floated. Some floated for 2 months and germinated afterwards. The seeds of *Citrullus vulgaris* and *Cucurbita maxima* were found drifted up on Volcano Island in the lake Bombon, Philippines.

It has long been known that Gourds and Calabashes have been found stranded on the Norway coasts, one at least of which contained seeds.

Cucurbitaceae, as a rule, are absent from oceanic islands, and those that do occur are usually small baccate ones which were doubtless conveyed by birds. It is probable that these floating Gourds fail to establish themselves on tidal mud or sandy or shingle beaches, hence their non-appearance in remote islands.

Luffa insularum, a variety of *L. cylindrica*, is sea-dispersed to a certain extent in the Polynesian Islands. In the *Luffas* the outer pulp of the Gourd dries up or decays on the plant, and the fibrous skeleton remains, the apical disc falls off and the seeds fall out, though frequently a few remain entangled in the fibres. Guppy found fruits like this floating in rivers, but says they only floated a few days, not more than a week. The seeds of *L. insularum*, at least, floated for months, but those of typical *L. cylindrica* sank in a few days. The former had an air-space in the seed cavity. In the latter the seed completely filled the testa. It is probable that others of these hard-shelled Gourds are drifted down rivers and dispersed thus by water.

UMBELLIFERAE.

Hydrocotyle vulgaris.—Praeger states that he finds the fruits of this float for 2 weeks, Guppy for some months. The plant is, however, apparently dispersed only locally by water, and owes more to attachment of the fruits to the feet of animals and birds.

In *H. verticillata*, of the Hawaiian Islands, the fruits float for weeks, and those of *H. asiatica* for months (Guppy). This latter was met with by the early botanists in New Caledonia. It is very common in damp ground all over tropical Asia, but I doubt if it has ever been dispersed by sea-transport. It seems generally absent from islands, and is, I think, dispersed only by rain-wash and by the adhesion of its fruits to the feet of animals and man.

Oenanthe.—Most of the riverside or aquatic species of this genus have floating mericarps, though their buoyancy is usually not of long duration. Praeger gives 2½ days for *Oenanthe fistulosa*, 1½ days for *Oe. Lachenalii*, 4 days for *Oe. pimpinelloides*, 1 week for *Oe. fluviatilis*, and over 15 months for *Oe. Phellandrium* (*Oe. aquatica*), for which Guppy gives from 1 to 4 weeks; *Oe. crocata* 6 months (Guppy). Of these, *Oe. fistulosa* and *Oe. fluviatilis* are submerged plants, and therefore it would be of importance that, as the plants inhabit rather deep water, the fruits should sink after a short buoyancy. However, fruits of *Oe. fistulosa* floated from August 30th to September 12th, when all sank. *Oe. crocata* and *Oe. Lachenalii*, common on the Thames river bank, float very well, and are regularly dispersed by river. When the fruits are ripe, in autumn, they are blown into the water, and after drifting down are stranded on the banks by the fall of the tide or lowering of the river, and soon spring up. Floods also distribute these fruits widely over low-lying wet ground, ditches and marshes. The buoyancy is due to the corky lateral masses on the mericarps. In *Oe. fistulosa* the seed completely fills the rather corky pericarp (Pl. XII, figs. 1 and 2, *Oe. crocata*).

Peucedanum palustre.—Birger found fruits of this plant floating in drift on Tjuron Island in Sweden. It is certainly a marsh and river plant, and is doubtless dispersed by water. The small fruit has the sides of the mericarps drawn out into corky wings.

Cicuta virosa.—This *Umbellifer* has small rounded mericarps with low ribs. The pericarp is thick in proportion to the size of the embryo. It is found on river banks and lakes. In the latter places I suppose it must have been brought in mud on the feet of birds, as the very small fruits are not too big to be carried in mud. The fruits, however, float, and Birger records their occurrence, with other seeds and fruits, in drift off Tjuron Isle, Sweden. The plant is northern and subarctic. It is found in Europe, Siberia to Kamschatka, Sachalin, China, Japan and Kashmir, and North America. It is recorded from river mouths in Kamschatka and from Khantak Island, Alaska. It is probable that it owes its wide northern distribution to both river- and sea-dispersal.

Sium latifolium.—This appears to be river-dispersed, as the mericarps float for some months and are very light. The pericarp is thick in proportion to the seed. *S. angustifolium.*—The mericarps float for some months (Guppy). The pericarp consists entirely of aeriferous tissue. In both of these the pericarp is thick and corky in proportion to the seed, and strongly 5-ribbed in *S. latifolium*, but comparatively smooth in *S. angustifolium*. They are ditch and stream plants.

Angelica sylvestris.—A riparian plant of which the fruits float for over 15 months (Praeger and Guppy). This is very common along the Thames banks. The body of the mericarp is small, but rather large in proportion to the embryo, the lateral wings are drawn out so that the whole fruit is rather flat and thin.

Archangelica officinalis.—The *Angelica*, a northern *Umbellifer*, is probably dispersed in the Arctic regions mainly by wind, but the fruits certainly float. It occurs as a garden escape on the Thames river bank, where it grows between the setts of the embankment, between Hammersmith and Barnes Bridge. It seems to have started from somewhere on the shore near the reservoir opposite Chiswick Mall, and the seeds have drifted up the river and established themselves in the wall near Mortlake Brewery, above the bridge, carried there by high tides. It is not a tidal-river plant, and it has failed to establish itself in the mud-banks. The mericarps are thick and corky, with 5 corky projecting ribs. The plant grows chiefly in the north temperate region within the Arctic circle, from Norway to Kamschatka, and in Labrador.

Of the other British *Umbelliferae*, *Ligusticum scoticum* and *Crithmum maritimum*

are sea-dispersed. Of the rest, fruits of *Pastinaca sativa*, *Heracleum sphondylium*, and *Coriandrum sativum* float 1 day, of *Daucus carota* and *Myrrhis odorata* 2½ days, *Smyrnium olusatrum* 3 days (Praeger). *Myrrhis* is a typical river-bank plant in the north of England and Scotland, and is no doubt spread along the streams in this way. *Daucus* grows usually in dry spots, and is either blown along or carried by adhesion; even the maritime form does not appear to be spread by water. Those of *Smyrnium olusatrum* and *Physospermum cornubiense*, which float 1½ days, owe their little buoyancy to the pulpy or swollen pericarp. I do not think either are likely to be water-dispersed, as they inhabit dry spots.

CORNACEAE.

Cornus suecica.—Praeger says the seed of this plant will float 1 week. It is a marsh plant, and might perhaps be dispersed by streams, but it is usually bird-dispersed.

CAPRIFOLIACEAE.

Both dry fruit and seed of *Viburnum lantana* will float 2 days (Praeger). This tree sometimes grows by streams, but it is more commonly an inland plant, bird-dispersed.

RUBIACEAE.

Dichilanthe borneensis.—Beccari (in "Nelle Foresti di Borneo") records finding the fruits of this plant floating on the lake at Kapuas. It is a shrub or tree, with the flowers in small terminal dense heads. In fruiting, the tube of the small bilobed calyx swells and is attached to the fruit. When ripe the fruit is nearly ¼ inch long, roughly pear-shaped, narrowed to the base and dilated on one side, terminated by the withered free portion of the calyx. A section shows that the 2 small ovules are on the straight inner face, the outer dilated portion is woody and contains a number of narrow air-spaces. The seed is certainly adapted for dispersal by water, and it is remarkable that it is so local. The only other species known is *D. zeylanica*, of moist low country in Ceylon. The ripe fruit of this is unknown, but as far as I can see from herbarium specimens, it has not this floating structure at all, and it does not appear to be associated with lakes or rivers.

Adina cordifolia.—An Indian tree with minute wind-dispersed seeds, of which 300,000 go to an ounce. This is distributed by rain and floods. The seeds are drifted to the base of trees, termite nests, embankments and ditches (Troup).

Lindenia.—These riverside shrubs have a somewhat remarkable distribution, as Guppy points out ("Notes of a Naturalist," p. 395). Two species occur in Mexico, 1 in Fiji and Samoa, and 1 in New Caledonia. *L. vitiensis* grows on the rocky banks of Fijian streams, heads of estuaries and torrents. All the species possess the Willow leaves so characteristic of plants of mountain streams. The capsule of *L. vitiensis* contains numbers of small angular seeds, about 1·5 mm. across, and 400 go to a grain. The seeds float buoyantly by reason of their crisp, air-bearing cellular tissue. When this is stripped off, the minute nucleus, barely 1 mm. across, sinks (Guppy). It is quite possible that these seeds when floating might be attached to the plumage of a bird, or carried in mud on its feet, which would account for its wide distribution, but I would suggest that this is a case in which the genus was formerly much more widely distributed, and many species have died out between these distant spots.

Galium palustre.—The very small fruits of this plant float from 2½ months

(Praeger) to 6 or 12 months (Guppy). It is an abundant plant in Europe in ditches and wet spots and canal banks, and is undoubtedly water-dispersed. The other species of this widely-distributed genus usually have non-buoyant fruits, or at most they float for 1 day only. They mostly appear to be dispersed by rain-wash or by adhesion to birds, etc. *G. aparine*, mainly spread by its adhesive stems and fruits, is said by Sernander and Norman to possess a considerable buoyancy in the fruits from the hollow cavity in the seed. Guppy found them floating in autumn river-drift in England, Norman found fruits drifted on Scandinavian beaches, and Birger in river-drift in Sweden. According to Praeger, they float but 12 hours, Guppy says a few days. It is probable that this rather dry locality plant is not to any extent water-dispersed.

Rubia peregrina, the Madder.—The fruits of this float for 1 week, according to Praeger. I have never seen it near water, and this buoyancy must be quite adventitious.

VALERIANACEAE.

Valeriana officinalis.—This is a riparian plant, but dispersed by wind. Praeger says its fruits float for 3 days. These plumed fruits, falling or being blown into the water, therefore would not sink at once, and might readily be carried a long way down stream before they came to rest on the bank. It is a regular river-bank and marsh plant.

Valerianella.—Of these, *V. rimosa* is recorded as having fruits that float from 1½ to 2 weeks, the other British ones from 1 to 5 days, but they are all dry station plants. *Centranthus ruber* fruits float for 1½ days, but I have seen no evidence of this being water-dispersed.

DIPSACEAE.

Scabiosa succisa is reported by Praeger to float from 1 to 15 months. It also is a dry country plant, and unlikely to be water-dispersed. *Dipsacus sylvestris* 1 day, *Knautia arvensis* and *Scabiosa columbaria* 2½ days. These are also mainly dry land species.

COMPOSITAE.

A large number of the fruits of the *Composites* are plumed and generally wind-dispersed, but even of these some also float and, if blown into the water, may be carried further along. Kronfeld shows that in plumed fruit such as that of *Taraxacum* the achenes float longer with the pappus attached, even when the hairs are closed together. Small says that the closed pappus usually encloses an air-bubble and acts as a float. *Compositae* with plumed achenes are often abundant on river banks. Such are *Senecio aquaticus*, *Sonchus palustris*, *Aster tripolium*, *Pluchea indica*, but these appear to be more distributed by wind than by water. Guppy gives none of the plumed *Compositae* as floating at all. Praeger, however, gives a number as floating for some days, a few as floating for over 1 week, and one, *Helminthia echioides*, for 15 months or more. Birger gives the following plumed achenes as floating in the Falkland Isles :—

Aster Vahlii, of 100 achenes 10 floated for 30 days.
Baccharis magellanica, of 52 achenes 7 floated for 5 days.
Chabraea sp., of 100 achenes 26 floated for 1 day.
Hypochaeris arenaria, 8 floated 1 day.

Aster tripolium.—The achenes of this mud-flat species are plumed and can be dispersed by wind. They also float for 5 days (Praeger). But what is more important in their dispersal is, as is shown by Guppy, that they germinate

in sea-water, and the seedlings may be dispersed, as is the case in *Mimulus*, *Salicornia*, etc.

Cirsium arvense.—Achenes and stolons of this Thistle, introduced into South Africa, are carried down stream by floods and deposited on river banks, where they grow (Miss K. A. Lansdell in " Weeds of South Africa ").

Galinsoga parviflora.—This weedy herb is dispersed in the same way as *Cirsium* in South Africa, according to Miss Lansdell.

Praeger gives the following periods for British *Compositae* whose achenes float for 1 day and more :—

1 day	..	*Senecio aquaticus*, *Leontodon autumnalis*.
1½ days	..	*Senecio viscosus*, *Thrincia nudicaulis*, *Crepis biennis*.
2 days	..	*Solidago virga-aurea*, *Senecio squalidus*, *Carlina vulgaris*, *Hieracium vulgatum*, *H. anglicum*, *H. boreale*.
2½ days	..	*Onopordon acanthium*.
3 days	..	*Sonchus asper*.
3½ days	..	*Sonchus oleraceus*, *Carduus lanceolatus*.
4 days	..	*Taraxacum officinale*, *Sonchus arvensis*.
5½ days	..	*Senecio vulgaris*.
6 days	..	*Hieracium aurantiacum*.
1½ weeks	..	*Artemisia maritima*, *Carduus pratensis*.

Most of these live inland and are not specially adapted for water-dispersal. It is noticeable that the riparian *Senecio aquaticus* floats for a shorter period than any of the inland kinds. The achenes of *Sonchus palustris*, however, seem to be really adapted for river-dispersal and are therefore described separately.

Sonchus palustris.—This noble Sow-Thistle inhabits the muddy banks of tidal rivers in England at Aylesford and Snodland, and in Europe generally from Denmark to Russia and Serbia. It is about 6 feet tall, and the plumed achenes fly readily along the banks and into the river. The plume is very soon detached, and the achene is so modified as to float and be borne up or down stream, according to the tide. The achenes are 3 mm. long, considerably larger than those of *S. oleraceus*, which are 2 mm. long. They are covered with a loose, pale fawn-coloured pericarp, faintly rugose, with 2 prominent ribs on one side and a keel-edge. The whole achene is flat without processes, like those of *S. oleraceus*. In fact, it most resembles in shape, ridges and keels the fruit of one of the water-dispersed *Oenanthes* (Pl. XII, figs. 4 and 5). I have seen it growing along the tidal mud-banks of Aylesford, and in habitually flooded fields at Snodland, Kent, and it is clearly dispersed by the rise of river and by the floods over the river meadows.

Of the *Compositae* with non-plumed achenes, Praeger and Guppy give the following periods of floatation of the achene :—

1 day	..	*Achillea millefolium* and *A. Ptarmica*.
1½ days	..	*Inula salicina*, *I. crithmoides*, *Anthemis arvensis*, *Chrysanthemum segetum*.
2 days	..	*Inula Helenium*, *Anthemis cotula*, *Centaurea scabiosa*.
2½ days	..	*Pulicaria dysenterica*.
3 days	..	*Matricaria discoidea*.
From 6 to 12 months	..	*Bidens cernua*, *B. tripartita*, *Matricaria inodora* var. *maritima*.

The latter *Matricaria* is dealt with under Sea-Dispersal (*see* p. 297). The pond and river-edge *Bidens* have achenes covered entirely with an air tissue, and are regularly water-dispersed. They have also the advantage of having strongly adhesive sepaline processes, and are largely transported by animals.

Of the other *Compositae* of this section, the possibility of dispersal is small and limited to a few, which suggests that the main cause of the buoyancy of the plumed achenes is due to retention of air in the plumes of the pappus. But the dispersal of some of these unplumed achenes by streams and floods is clearly greater than is evidenced by these experiments. Thus *Tanacetum vulgare*, whose achenes are described by Praeger as floating 2 hours only, I find float for more than a day, and it is certainly a riparian plant dispersed by rivers, along the edges of which it can be found scattered. *Pulicaria dysenterica* is also a river-bank plant which certainly creeps gradually down stream along the edges, and its achenes must therefore be water-dispersed.

Centaurea solstitialis, according to K. A. Lansdell (*Journ. Dept. Agric. S. Africa*, xii, 344), is dispersed in South Africa by flood-water as well as by wind, and in grain. It is a widely-scattered plant which appears casually in England, by roadsides and in cornfields, and is undoubtedly introduced in grain into any temperate climate. Once there, it may spread by flood-water in countries liable to large rushes of water, like South Africa.

Ambrosia trifida, an American weed, has achenes with 4 or 5 spines. These are dispersed by water in Canada (Clarke and Fletcher, "Farm Weeds in Canada").

Tagetes minuta, a South American weed, and *Silybum marianum*, the Blessed Thistle, according to Lansdell, are also dispersed by water in South Africa. The Thistle has plumed achenes, but the seeds are rather large and the plumes not very big. It appears to me it moves about in my garden more by rain-wash than by wind. Both these plants were probably introduced into Africa in grain.

Franseria.—Fruits of a species found by Guppy on the sea-beaches in Chile, after being kept dry for 6 weeks, floated for from 2 to 4 days.

Xanthium strumarium.—In this plant the achenes are enclosed in an involucre covered with hooked spines, and are very largely dispersed by attachment to the fur of animals and the clothes of men. It is, however, also in flat open plains largely dispersed by water, floods, streams or rivers. Maiden records it as being so disseminated in New South Wales. Mr. Burtt-Davy writes to me :—"*Xanthium spinosum* and *X. strumarium*, and allied alien species are "common along streams in South Africa. This may be due to cattle, sheep, "goats, antelopes, etc., collecting there to drink and then rubbing off the "burrs, but I am convinced that the burrs are carried down stream by flood-"waters, then when the flood abates, the mud flats and sand-banks so common "along South African streams form an admirable nidus for the germination "of the seed, and you get luxuriant groves of these plants, covering every "available exposed place." The combination of animal- and water-dispersal of these plants is certainly the cause of the very wide dispersal of *Xanthium* all over the world.

CAMPANULACEAE.

Lobelia Dortmanni.—The seeds of this aquatic do not float, and the plant must be dispersed by the attachment of its seeds to the feet of birds and perhaps to deer and other mammals. It is, however, a lake plant, and it would derive no advantage from buoyancy of seeds.

Campanula rotundifolia.—Seeds float 1 day (Praeger). No doubt all the species of this genus are dispersed mainly by rain-wash and to some extent by wind.

ERICACEAE.

Arctostaphylos Uva-Ursi.—Dry fruits float for 1½ weeks (Praeger). The fruits are dispersed normally by birds.

Erica vagans.—Seeds float for $3\frac{1}{2}$ days (Praeger), those of the other species not at all, or for only 1 or 2 hours.

Pyrola minor.—Seeds float $2\frac{1}{2}$ days (Praeger). This is a damp heath plant, but the seeds are apparently only dispersed by rain-wash and wind.

GENTIANACEAE.

Limnanthemum (*Villarsia*) *nymphoides.*—In this aquatic the fruits do not dehisce, but are first detached by the decay of the pedicel. They float for some time. Mrs. Arber found them still quite green floating on water, and the seeds unripe and white on October 1st. By November 24th they were all bursting, and the seeds appeared ripe. Ravn says the pericarp rots and the seeds sink, but if separated from the fruit and thrown on the water, they float by the long hairs which cover them, enlarging their surface area without increasing their weight. If the hairs are removed, a slight shake causes them to sink, while with the hairs still attached they require a strong shake. Guppy (in "The Thames as an Agent for Plant Dispersal") shows that the seeds will adhere to a duck's plumage and can be so carried about, but he points out that the seeds of other species are not fringed with hairs. He records its floating from 1 to 4 weeks. The seeds in rivers, or, rather, still waters, would readily be carried to some distance before sinking, and the fruits, before dehiscing, more readily still.

Menyanthes trifoliata.—Seeds float for 2 months (Guppy). I believe also the fruits are eaten by ducks and the seeds so dispersed. It is a marsh and pond plant mainly. The seed's tegument consists of aeriferous tissue with intercellular spaces (Ravn).

BORAGINEAE.

Symphytum officinale.—The nucules of this plant float for $2\frac{1}{2}$ days (Praeger). This is a riparian plant, and it is difficult to see how it gets along the water edges unless by the floating of the nucules.

Myosotis caespitosa.—The nucules float for $4\frac{1}{2}$ days (Praeger). This is a waterside plant, and is no doubt dispersed by the flotation of its nucules. *M. scorpioides* (*M. arvensis*).—Nucules float for 1 day only (Praeger). A dry locality plant.

M. palustris.—It is curious that this truly riparian plant is said by all to have non-buoyant nucules. It is certainly water-dispersed, and frequently by detached branches which are floated along and grow when stranded. I have seen, however, plants recently appearing near Kew Bridge, which I can hardly think, from their position, could have been brought down the river and to have established themselves in this way. The nearest locality I know for the plant is near Teddington, about 5 miles away. The plants were growing in cracks between the stone setts, where fragments of the plants are hardly likely to have lodged.

Tournefortia argentea, *Cordia*, and *Mertensia maritima* are sea-dispersed.

SOLANACEAE.

Solanum dulcamara.—Praeger and Guppy say these seeds and fruits are not buoyant, but Birger found seeds floating in the drift off Tjuron Island. I notice the plant appears between the stone setts of the river bank near Barnes, below high-water mark, but it is possible that the seeds have been bird-deposited there. *S. rostratum*, of South America, is believed to be flood-dispersed by its fruits.

Datura Stramonium.—Seeds are carried down stream by flood-water and deposited on banks of rivers in South Africa, where they germinate (K. A. Lansdell).

Atropa belladonna.—The fruits float for 1 day (Praeger). I have found a plant of this growing on the edge of one of the Norfolk Broads, but it is usually a chalk-down plant.

Hyoscyamus niger.—Seeds float for 1½ days (Praeger). This is hardly likely to be water-dispersed.

Nolana, probably *N. paradoxa*.—Guppy found drupes of this plant on the beaches of Southern Chile. They have at first a fleshy covering, which disappears when lying on the sand, leaving angular stones 5 to 6 mm. across. Inside the hard outer coat is a layer of spongy tissue which gives it buoyancy, but this hard covering is absent at the scars of basal insertion, and the embryo seems insufficiently protected for a sea-water flotation. He found that 30 per cent. floated after 3 weeks in sea-water, and, after drying for nearly 1 year, almost all floated for 3 months. Two germinated after floating 6 weeks. This is possibly sea- or river-dispersed, but evidently not very extensively, as it is local.

OLEACEAE.

Fraxinus excelsior.—According to Praeger, the samaras of the Ash float for 3 days. This is not an uncommon plant along stream banks. I have seen them growing far from other Ash trees, along the river bank of the Thames, with the river-dispersed Alders. It would certainly travel faster over a country by rivers than by wind-dispersal.

APOCYNACEAE.

Ervatamia (*Tabernaemontana*).—Fruits of a species were found in sea-drift in the Moluccas by Moseley. They are mainly bird-dispersed, but might be carried down streams.

Ochrosia and *Cerbera* have fruits modified for sea-dispersal, and are treated of under that head (*see* p. 299), as are also the remarkably modified tidal river genera *Finlaysonia* and *Sarcolobus* (*Asclepiadaceae*).

LOGANIACEAE.

Fagraea Berteriana.—A tree, native of Fiji. Guppy says the fruits float for a few days. The fruit is a rather soft berry about 1 inch long, ovate. Nearly all this class of fruit is dispersed by birds or bats, but it is possible that this one may also be stream-dispersed.

SAPOTACEAE.

Bassia Motleyana (Illipe Nuts).—The sapotaceous trees have berries containing one or more hard seeds, and are mainly dispersed by birds or mammals. The Illipe nuts are dispersed by water also. They fall into streams in the Malay forests and are drifted down, often in great abundance. As they float the Malays catch them in nets for trade purposes.

Lucuma sp.—Seeds of this were picked up on the shores near Salcombe, Devon (Guppy), having been brought there by the Gulf Stream.

Maba sp. (*Ebenaceae*).—In Fiji the seeds float from 1 to 2 weeks (Guppy).

Halesia tetraptera (*Styraceae*).—The 4-winged fruits certainly float for about 4 days, after which they become water-logged and sink. They are mainly wind-dispersed.

PRIMULACEAE.

Lysimachia thyrsiflora.—This is a marsh plant growing in ditches and by canals. Birger found seeds of it in drift off Tjuron Island in Sweden. Guppy says they float from 1 to 4 months. They are angled and a few in a capsule.

L. vulgaris.—This is also a riparian plant. The seeds, 3 or 4 in an ovoid capsule, are discoid and covered with a pulverulent coat which soon rubs off. Praeger says they float only 1 day. I found they floated for 1 week or more, and Guppy says from 1 to 4 weeks.

Hottonia palustris.—The seeds of this are non-buoyant and sink at once, but it is said that they germinate under water and are dispersed as seedlings. It is also dispersed by water vegetatively.

OROBANCHACEAE.

Orobanche rubra, *O. picridis* and *O. minor.*—The seeds of these plants float for 2½ days, those of *O. hederae* 2 days, and those of *O. caryophyllea* 4 days (Praeger). *Lathrea squamaria* seeds float 2 days.

The buoyancy of the seeds of these plants can have little importance in dispersal, as they are all inland plants of dry situations. Still, the seeds of the *Orobanches* might in some circumstances be dispersed by floods.

SCROPHULARINEAE.

Linaria vulgaris.—In this plant the capsule opens at the top. The seeds are discoid with a circular wing, and as the plant is a habitant of dry open spots, this wing serves to aid in wind-dispersal. However, they float for 3 or 4 days.

Pedicularis palustris.—The seeds float for from 1 to 6 months (Guppy). This rather tall plant is found in marshes, and I have seen it in the Broads, where it was evidently water-dispersed. The seeds possess an air-cell structure in the testa (Ravn). The dwarf moorland species, *P. sylvatica*, has non-buoyant seeds.

Rhinanthus crista-galli has rather large seeds which float for 6 months (Guppy). It is a grassland plant, but may be dispersed by floods.

LENTIBULARIACEAE.

Utricularia is usually dispersed by the floating away of portions of the plant, or by their being attached to the feet or bodies of birds, or by the flood-dispersal of their winter buds. Mrs. Arber says, however, that the seeds of *U. minor* float on the water, as the seed-coat is pitted and capable of retaining air-bubbles for a long time. Eventually they lose the air and sink.

CYRTANDRACEAE.

Most of these, having very light seeds, are dispersed by rain-wash, and a few by wind. Guppy states that the seeds or fruits of several species of *Cyrtandra* of Hawaii float for a few days. These, however, are not waterside plants.

BIGNONIACEAE.

The greater number of these plants have winged seeds dispersed by wind. Some of these light seeds may, however, float in rivers as well, for a short time at least. *Oroxylum indicum* was abundant along the Pahang River and the round-winged seeds were to be seen floating in the water. As it grew

in muddy spots near the river-edge, I conclude it may be to some extent dispersed along the river banks by water. The oblong-winged seeds of *Catalpa bignonioides* I found sank in less than 2 days. *Dolichandrone Rheedii*, of tidal rivers in tropical Asia, is treated of under Sea-Dispersal, p. 308. It is distinctly adapted for water-dispersal.

The Calabashes (*Crescentia*) are natives of South America. They have gourd-like fruits containing a quantity of pith, in which are embedded a number of seeds, and Guppy records the occurrence of these fruits drifting in the rivers of Ecuador and the West Indies. The fruit is often met with in sea-drift also, and there is reason to believe that it has been found among the Gulf Stream drift on the European coasts; but as none appear to have successfully traversed the sea, I have excluded them from sea-dispersed plants. When the fruit is detached from the tree, the pulp soon becomes soft and black, and eventually dries up, and the seeds decay unless the shell breaks and they are released. The fresh seeds are buoyant at first, as the embryo only partly fills the testa, but when dry they merely float for a day or two. The fruits both of *C. cujete* and *C. cucurbitina* float from the lightness of the spongy pulp in the interior. Though these fruits do not pass across the seas in sufficiently good condition for their seeds to germinate, they are certainly river-dispersed. Guppy, whose account of these fruits I have largely drawn upon, says :—" The occasional presence of a solitary " wild specimen of the Calabash tree among the vegetation bordering the beaches " on the Black River (Jamaica) may thus be explained, the parent gourd having " been brought down the river." The tree, of no great size, usually seems to grow in damp spots by rivers, but it will grow in dry spots as well. The seeds of *C. cucurbitina* are rather large and flat, and appear from dried specimens to have a space between the cotyledons. Those of *C. cujete* are small, subtriangular and flat. It is possible that both may be dispersed by water to some extent.

CONVOLVULACEAE.

Many of these plants are sea-dispersed and will be found under that section. *Calystegia sepium*, which is also sea-disseminated, is sometimes to be found along rivers, where it has been brought by its floating seeds. *Aniseia uniflora*, of the tropics, and *Merremia vitifolia*, a typical river-bank plant, are probably more readily dispersed by river than by sea. *Convolvulus arvensis* has seeds which float about 12 hours. It is more readily dispersed by its long rhizomes than by any other way. Guppy kept seeds of *Calystegia sepium* afloat for 33 months, of which the first 9 were in salt water, the rest in fresh water. At the end of this period 1 seed germinated healthily in fresh water. I refer the sea-dispersed *Convolvuli* to the section dealing with Marine Dispersal, pp. 302–307.

VERBENACEAE.

Tectona grandis (Teak).—Troup writes of this :—" The chief transporting " agency is water, and this accounts for the fact that the Teak often " springs up gregariously on alluvial flats, whither the seeds are conveyed " in the season of floods and deposited in quantity. On hillsides many are " washed down. The fruit is globose, with a pithy covering enclosed in a bladder-" like calyx. Rain is the chief agent in burying the nuts, but white ants eat the " felty covering, and no doubt assist to bury them."

The tree is a native of Assam and Burma, and has been introduced into Java and other parts of tropical Asia, where it grows in rather dry open woods.

Verbena officinalis.—Praeger states the fruits of this float for 3½ days. It

sometimes grows by rivers, but more usually in dry spots, and is dispersed regularly by adhesion to passing animals.

Species of *Premna*, *Avicennia*, *Clerodendron* and *Vitex* are sea-dispersed.

Hosea Lobbiana.—This is a kind of climbing *Clerodendron* with fruits remarkably modified for water-dispersal. The common *Clerodendrons* have small baccate fruit of 4 carpels, usually dark blue or black, surrounded by an accrescent star-like red calyx, and are dispersed by birds. In *Hosea*, the carpels of which, often 2 separate ones, persist in fruit, are elongate horn-shaped bodies of a dark purple colour, dilated in the middle, about 2½ inches long and ½ inch through. The purple pericarp of each is leathery and contains 1 long cylindric seed. The plant climbs over bushes in the wet river swamps of Sarawak, Borneo, practically growing in the water, into which the pendulous fruits drop and are borne away.

LABIATAE.

Mentha aquatica.—This Mint, so abundant on river edges, possesses the longest-floating nutlets of any species recorded. The nutlets, which are shaken out of the calyx by wind or fall of the plant in autumn, on dropping into the water are readily drifted away. They possess an outer coat of a dry fleshy substance composed of air-cells with thin walls (Ravn), and float for from 6 to 12 months (according to Guppy).

In *M. gentilis* the nutlets float for 5½ days, and those of *M. arvensis* for 1½ days, according to Praeger, who found that those of *M. longifolia* and *M. Pulegium* did not float at all. The last three species are not riparian, and could hardly be benefited by any power of floating.

Lycopus europaeus.—This little plant is specially adapted for dispersal by river, and is very common on English river banks, where it is rapidly dispersed. It is one of the most common plants on the banks of the Thames between Richmond and Kew, and may often be seen growing in cracks in the brickwork of the walls, into which its seeds have been drifted by high tides. The nutlets are obcuneate and roughly triangular, and half surrounded from the base by a corky float (Pl. XII, figs. 7 and 8). They float for from 12 to 15 months (according to Praeger and Guppy).

Scutellaria galericulata.—This riverside plant possesses a raceme of flowers of which the 2-lobed dry calyx in fruit encloses the 4 nucules. The upper lobe of the calyx closes over the lower part, which contains the nucules. When ripe the shaking of the stem by the wind causes the calyx-lobes to separate and permits the nucules to be thrown out. They are small, yellow, and densely covered with thick processes (Pl. XII, fig. 17). Being very light, they float for 12 months (Guppy). The plant grows on the edges of rivers throughout Europe, and is common along the Thames. I have found it growing in large tussocks of *Carex* by Virginia Water, where the nucules must have been drifted by a rise in the water. The processes on the nucules of this plant are longer and more prominent than in other species of the genus, and form anchors by which the nucule is retained when it reaches a suitable position among the herbage at the water's edge. Praeger states that the nucules of the rarer *Scutellaria minor*, which is more of a pond than a riparian plant, do not float. The nutlet integument of *S. galericulata* consists of aeriferous tissue with intercellular spaces (Ravn).

Stachys palustris.—The nucules of this riparian species, common along our river-edges in England, float and are dispersed by water. They will float for from 1 to 6 months (according to Guppy), and over 15 months (according to Praeger). The seedlings also float.

In none of the other species of *Stachys*, so far as is known, do the nucules float for over a day. They are all inhabitants of dry spots.

Few of the other *Labiatae* have floating nucules. Praeger records those of *Salvia pratensis* as floating 6 days, of *Clinopodium acinos* for 2½ days, *Galeopsis Tetrahit* for 2 days, and *Origanum vulgare* and *Stachys officinalis* for 1 day. Those of *Leonurus sibiricus* float to some extent, but the stout spines of the calyx are readily attached to clothing, and its wide dispersal is certainly due to this. It is an inland plant.

CHENOPODIACEAE.

Salsola Kali.—This plant is very widely distributed over the world. Guppy affirms that the fruit sinks, but when the plant dries, the fruit is often detached with the perianth, and floats in sea-water for a few days. Portions of the plant bearing fruits sank in 10 days. Praeger found that the seed sank at once, and the dry fruit floated only for 5½ days, Guppy says from 1 to 4 weeks. There is no doubt that the plant is dispersed on the mainlands by floods. Burtt-Davy writes to me that he has driven through a small forest of *Salsola Kali* var. (an alien) in mud flats at the mouth of one of the rivers in the Cape Province, South Africa, which plants must have been brought down by water. It was introduced into Fremont, County Colorado, in 1892, and a freshet in the Arkansas River in 1894 with the irrigation water carried its seeds in one season over many farms in the valley, as far as the eastern line of the State. It has since spread nearly one-third of the way across the State of Kansas and over irrigated lands along the Platte River, Colorado, and the Snake River, Idaho. It was introduced in flax seed, oats, wheat and alfalfa into Dakota (Lyster in " Migration of Weeds "). There is little doubt that the seeds of this plant, known in America as the Russian Thistle, can be dispersed by water in spite of their rather poor buoyancy, in floods at least, over very large areas with some rapidity. It probably owes its wide distribution in distant sea-coasts and islands to its being imported in ballast and in cereal grain. In 1926 it appeared on the banks of the Thames between Kew and Mortlake, in the gravel used in making an embankment. The seed was probably brought in gravel from the mouth of the Thames. The plant is found as a seashore plant in Europe, the Azores, Madeira, Canaries, and from Morocco to Egypt, in inland plains or steppes in Afghanistan, Thibet, North India, Mongolia and China, in North America, Chile and Argentina, and in Australia as early as 1802, no doubt imported. It seems clear that it had its original home in temperate Asia and Europe, but while in the latter area it is mainly now a seashore plant, in the former it inhabits the inland steppes. It may have reached the islands by sea, but more probably in ballast or cereals. It has also moved over the plains in Siberia and America as a tumble-weed.

Chenopodium.—Few of these have floating fruits. They are mostly inland plants of dry habitat. Praeger gives of *Ch. hybridum*, fruits float 1 day; of *Ch. murale*, from 2½ to 7 days; of *Ch. rubrum*, from 3½ to 4 days; of *Ch. album*, for 4½ days.

Atriplex patula.—This sometimes grows by the sea, but is more common inland. Praeger found that its seeds sank at once. Guppy gives a buoyancy period of from 6 to 12 months; possibly this was based on a maritime form. There are several species of this genus which frequent the sea-coasts, and which are probably sea-dispersed—*A. littoralis*, *A. portulacoides*, *A. pedunculata*, etc.—but I can find no account of their methods of dispersal. In *A. portulacoides* the perianth is large and swollen, and may serve as a floating organ, but I find that when ripe the small fruits usually fall out.

Suaeda.—The seeds of all species appear to sink very speedily. Praeger states that those of *S. maritima* float for 2½ days only. However, the species are very widely distributed. *S. fruticosa* in sea marshes is found in Europe,

Algiers, Morocco, Egypt, Madeira, Canaries, Palestine, Afghanistan, India, Arabia, Somaliland, Benguella, St. Helena, and apparently introduced somehow into Argentina. It is clearly indigenous in St. Helena and in Madeira and the Canaries, but it is rather difficult to see how it got to these spots, possibly in mud on the feet of birds frequenting the sea marshes, or by birds swallowing the seeds, as Dr. R. Brown says (in "Our Earth and its Story," 1888) he found a seed like that of a *Suaeda* in the gizzard of a snow-bunting.

POLYGONACEAE.

Polygonum.—Guppy gives none of these as having buoyant nutlets. *P. hydropiper* is a very widely distributed plant occurring all over the world, even in the tropics. It nearly always grows by stream edges, and is certainly water-dispersed. The nutlets are polished black and lenticular. Praeger gives their buoyancy a week's duration. I have found them float generally for 2 or 3 days only. The plant is common along the River Thames by Kew Bridge in muddy spots, where it has certainly been brought by the stream. *P. persicaria* has nuts similar to those of *P. hydropiper*. These float in a similar manner, though Praeger gives only 1 day's buoyancy. It also occurs in similar spots on the Thames bank, where the seed has evidently been brought by water. *P. lapathifolium*, the nutlets of which are said by Praeger to float for 1 day, also occurs on the mud-banks of the Thames near Kew, obviously brought by the river. *P. tomentosum* (*P. maculatum*) he gives a buoyancy of 3 days, and the widely distributed *P. minus*, also like *P. hydropiper* very widely dispersed throughout the world, for 1½ days. *P. aviculare*, with its non-buoyant triquetrous nuts, is a dry inland plant, but the allied seashore *P. Roberti* (*P. Raii*) has nutlets which float for 1½ months.

Rumex—The Docks are dispersed by several different methods by the aid of their accrescent sepals. They are disseminated largely by wind. In many cases the edges of the sepals are spinescent and serve to attach them to passing animals or clothes of men, but they are also largely dispersed by water. The enlarged papery sepals frequently possess a floating organ in the shape of a corky boss on one or more of the sepals. One of the commonest species is *R. conglomeratus*, which has three of these corky floats on the sepals. The fruits float for as long as 15 months (Praeger and Guppy), and the plant is common along all rivers as well as roadsides. Besides this, it is dispersed, like other species, by the rhizomes washed out of the banks being carried further down stream. *R. crispus* is another common species which has usually only a float on one sepal (Pl. VII, fig. 11), but sometimes one on each. Guppy records its fruits as floating for from 1 to 6 months, Praeger for 15 months. *R. sanguineus* has only 1 tubercule on the fruit. It floats for 2 months (Praeger). *R. obtusifolius* is a plant of drier localities. Its sepals are spiny. According to Praeger, its fruits float only 2½ days, and the more spiny-fruited *R. pulcher* has fruits which float for only 12 hours. *R. hydrolapathum*, the Water Dock, has the fruits hardly provided with floats. However, Guppy records them as floating for 12 months, and Birger found them floating in drift off Tjuron in Sweden. *R. domesticus* (*R. aquaticus*) certainly sometimes grows near rivers. The fruit is not tubercled at all. Guppy says they float for some months. I have found this plant on shingle beaches along the Tay, but it might have been brought there by the floating of its rhizome. *R. acetosa*, the Sorrel of our pastures, and *R. acetosella*, the Sheep Sorrel with non-accrescent perianth, do not float for a day.

The corky float, so important in water-dispersal, is an evolution during the ripening of the fruit of the mid-nerve of the sepal. It is hardly visible as a thickening during the flowering period, and only develops later.

MYRISTICACEAE.

Myristica.—The seeds of the Nutmegs owe their main dispersal undoubtedly to their being swallowed by birds for the sake of the aril (Mace), but in the forests certainly a number of the fallen seeds, like those of many other trees, are carried about by rain and rushes of water. Lewis says that the seeds of the Ceylon *Myristicas* (*M. Irya*, *M. Horsfieldia*, etc.) are dispersed by water. Guppy found the unopened fruits floating in sea-water off the Solomon Islands, but he says that, after dehiscing, the ripe seeds sink. Gaudichaud found seeds of 3 or 4 species floating off the Moluccas. The seeds of 2 species in Fiji Guppy found floated for from 3 to 7 days. It is quite clear that the seeds do not survive long immersion in the sea, but the trees may be diffused through the forests by streams, and so supplement the action of the fruit pigeons.

EUPHORBIACEAE.

Comparatively few of this large order seem to be disseminated by water other than rain-wash. Of the few English species, *Buxus sempervirens* has seeds which are stated by Praeger to float for 6 days, but the plant is strictly an inhabitant of dry hillsides, and the buoyancy of its seeds must be considered as adventitious. Of the large genus *Euphorbia*, *E. paralias*, *E. atoto*, and perhaps some other seashore species, are widely sea-dispersed. The seeds of *E. hiberna* are recorded by Praeger as floating for 5 days, and those of *E. portlandica* 2½ days, the seeds of *Mercurialis perennis* for a single day. The others do not float at all. Of tropical plants, the seeds of *Omphalocarpus*, *Ricinus* and *Excoecaria* are sea-dispersed and are described under that heading on p. 314.

Hevea braziliensis, the now well-known Para rubber tree of the banks of the Amazons, is a river-dispersed plant of some interest. The large 3-carpelled fruit contains a single large seed in each cell of the capsule. When ripe the capsule explodes with a sharp report, throwing each seed to a considerable distance. Should the seed strike a log of wood or hard ground, it bounds along further till it strikes a patch of mud, where it is embedded about half its length in a sloping direction, and speedily commences to germinate. If it falls into the river, it floats away, being very light, the buoyancy being due to its soft pithy cotyledons, though the testa is also light enough to float. Eventually it may be stranded on the shore, where it may germinate. Under these circumstances the seed may float for about a week, as the seeds do not retain their vitality longer in ordinary circumstances. I may digress to point out that the silvery markings on this and the other *Euphorbiaceous* seeds (*Ricinus*, *Jatropha*, etc.), giving them some resemblance to a beetle, are not (as Lubbock and some others have suggested) intended to induce a bird to carry them along in mistake for an insect. This colouring is merely cryptic. In the case of *Hevea* the seeds are very attractive to pigs, deer, and rodents, who devour them greedily, and the silvery marks, by more or less resembling streaks of light falling on the brown ground, cause these animals to overlook some of the seeds. It is probable that most of the other species of *Hevea* have also buoyant seeds, but I have no evidence of this.

Trewia nudiflora.—A globose pale green berry from 1 to 1½ inch in diameter, with 4 seeds and a pulpy, fleshy yellow aril, buoyant in water and disseminated thereby. Germination is best effected when the fruits and seeds are partly buried, as they are in alluvial plats (Troup). It is an Indo-Malayan tree.

Homonoia riparia.—This Willow-like shrub with small seeds grows in shingle in rivers, and often on islands therein, and is doubtless river-dispersed. It is abundant in the Indian and Malayan regions.

URTICACEAE.

Few plants of this order appear to be dispersed by water, and they are usually absent from river banks or wet situations. The small fruits of the Pellitory, *Parietaria ramiflora*, are said by Praeger to float for 3 days. The plant certainly occurs on walls below the high-tide mark of the river at Kew, and the fruits may have been drifted there by water. Fruits of the Hop (*Humulus Lupulus*) float for 3 days, and those of the Elm (*Ulmus campestris*) for 5½ days (Praeger), but these are not likely to derive any benefit from this buoyancy.

The fruits of the Mulberry (*Morus alba*) are said (by Troup) to be dispersed by water in India, and of *Ficus hispida* he writes :—" This tree has been " introduced into the Changa Manga plantation, near Lahore, by water." I have also seen this Fig tree growing in cracks of the stonework in the stream at the Residency in Penang, where it must have been brought by water. Guppy states that the figs (or the seeds) of *Ficus Harveyi* and *F. scabra* in Fiji float for from 7 to 10 days. Both the Mulberry and the Figs are distributed mainly by birds and bats, but they may be casually dispersed by water also. Of *Artocarpus integrifolia* Merrill records finding a head containing ripe seed drifted up in good condition on Volcano Island, in Lake Bombon, Philippines.

SALICACEAE.

Many of the Willows frequent borders of streams, and their fluffy seeds drift about in the wind till they come to rest on a suitable muddy spot, but they are not, to any large extent apparently, aided by water-dispersal. Of *Salix pentandra*, the seeds (according to Praeger) float for 1½ days, and those of the creeping mountain *S. reticulata* for 2½ days.

Populus deltoides, the Cotton-wood of North America, is, however, water-dispersed as well as wind-dispersed. A. W. Williamson (" Cotton-wood in Mississippi," *U.S.A. Agric. Bull.*, 24, p. 16) says the seed is distributed by the overflow waters, which frequently leave fertile seed on the muddy alluvial flats, far from the parent tree. " Seeds germinated very rapidly, and after " 3 weeks old 50 per cent. germinate."

Salix fragilis and *S. alba*.—The slender spikes of fruits fall off and float down the river before the capsules dehisce. When stranded, the capsules open and let out the plumed seed as soon as the fruit gets dried. I have seen immense numbers of the spikes drifted up along the shores of the Thames at Reading and elsewhere with the capsules dehiscing and some unopened. The plume of the seed, when wetted, serves to detain the plant on the mud, and thus the tree may be spread readily along the river edge both by water and wind.

BETULACEAE.

Alnus.—The Alders, like the Birches, have short cones of numerous bracts, containing in the axils of the bracts small, flat, more or less winged fruits, obovate or lanceolate in outline and about 3 mm. across. The common English Alder has obovate, flattened fruits, in which the edge is not expanded at all into a wing, but in many American and temperate Asiatic species there is a distinct wing to each edge, fairly large in *A. cernua* and some others. There is a great variety of stages of development of the wings from the merely flattened edge of the fruit of *A. glutinosa* to the distinct rounded wings of *A. cernua*, but none have the body of the fruit reduced and the wings so developed as those of the wind-dispersed Birches (*Betula*).

The fruit of the English Alder is somewhat corky when dry, and floats

very easily for 12 months (Guppy). The plants are commonly dispersed by water, and very characteristic of wet ground and river banks. Trees can be seen in the walls of the ditch along the Thames at Kew, derived from fruits drifted up by high tides, which found a lodgment in cracks between the bricks. Very large numbers of these little red-brown fruits are produced by a single tree, and in the autumn can be seen floating in immense abundance in the rivers and ponds. There is no trace of a wing in the fruit, which, with the exception of the seed, is corky all through. It has much the shape of the fruit of a Nipa Palm.

The Alders are widely diffused from Europe over temperate Asia to North India, China and Japan, in America as far north as Greenland and south to the mountains of Peru and Bolivia. They do not appear to be able to cross the sea, as they are absent from the Azores, Canaries, etc., though Guppy records the fruits as abundant frequently on sea-beaches and estuaries, where they have been drifted down with the other river-drift. However, it is hardly likely that they would thrive on sea-beaches or tidal mud even if they reached islands.

The evolution of the wings in the wing-fruited forms may serve to drift the seeds into the water of the rivers from the trees, but many grow in marshes, and the fruits may thus merely be dispersed by wind, as in the case of the Birch.

Betula alba.—In the little fruits of the Birch the body of the fruit is reduced to a much smaller size than in most species of Alder, and the wings are larger in proportion. They are mainly dispersed by wind, for which they are well adapted, and, as open-heath trees, are readily blown to considerable distances over moorland. According to Praeger, they float for 2 days only, and some which I tried floated only a few days; but in 1928 I found, at the end of February, very large numbers of Birch fruits floating in the lakes in Kew Gardens, accompanied by Alder fruits. Some also were resting on floating leaves. These fruits must have been shed in December at the latest. I brought a large number home and kept them floating till the first week in March, when they all became water-logged and sank. The Alder fruits with them remained floating. These Birch fruits must, therefore, have floated for at least 2 months and probably 3. The fruits are also carried along the ground by rain-wash, but in many places in Scotland and elsewhere trees may be found along stream edges which have certainly taken their rise from water-borne fruits.

The dwarf arctic Birches, *B. nana*, etc., have wingless fruits, probably because the plants are too stunted to derive any advantage from the wind.

MYRICACEAE.

Myrica Gale.—Most of the *Myricas* have baccate fruit and are dispersed by birds, but the English Sweet-Gale (*M. gale*) has a very small dry fruit, which (according to Praeger) floats for from 14 to 15 months. The small fruits are enclosed in the floral scales, which may serve to add to their buoyancy. As the shrub, however, is rather an inhabitant of moors in somewhat dry spots, though not uncommon around marsh pools, I suspect the fruits are more dispersed by wind than by water.

AMENTACEAE.

Corylus avellana.—Hazel-nuts sink when fresh (according to Darwin, "Origin of Species"), but after drying for a long time they floated for 90 days and subsequently germinated. The floating power is due to the shrinkage of the kernel. Hazel-nuts are common in the sea-drift on beaches in Europe,

but as the bush seldom grows on seashores, it is unlikely to migrate far. It is not uncommon on river banks, however, and may be dispersed by stream.

Quercus.—The acorns of the Oaks also float to some extent if dry. Guppy found from 4 to 8 per cent. of ripe fruits floated in fresh water, and about 10 to 12 per cent. in sea-water, but all sank in a day or two. Of some kept for 7 months, 20 per cent. floated after 4 weeks in sea-water, and 15 per cent. after 10 weeks. The buoyancy is due entirely to the cavity left by shrinkage of the kernel. He never saw a sound fruit in the sea-drift of England or Sicily. This refers to *Q. robur*, the English Oak. It is quite possible that these acorns may be dispersed along river banks, but it seems clear that no species can be sea-transported. The acorns of tropical species occur abundantly in sea-drift. Moseley records them 70 miles off the New Guinea coast, Guppy on Cocos-Keeling and on Java coasts, as does Schimper, and Penzig found them on Krakatau, but all appeared to be dead. Indeed, it is not probable that they could grow on seashores. However, *Q. virens* and a variety of *Q. phellos*, of North America, do occur on beaches or close to the sea. Along shallow river edges Oaks might readily be disseminated by the floating—or rolled along—acorns. However, neither nuts nor acorns can owe much to water-dispersal.

MONOCOTYLEDONES.

HYDROCHARIDACEAE.

Ottelia alismoides.—This aquatic plant, which grows in wet rice-fields and pools in warmer Asia, possesses capsules which float to the surface of the water, and by special disintegration discharge the seeds (Yoyo Makoyima). I have little information as to the dispersal of this plant, but, like many of the order, it is sometimes drifted about whole, though clearly the seeds themselves may be floated about.

ORCHIDEAE.

The Orchids derive little benefit from water-dispersal, but I have mentioned elsewhere the drifting of whole living plants in the sea (p. 253).

SCITAMINEAE.

Few, if any, of these plants are dispersed by water. Guppy records finding fruits of *Riedelia* floating in sea-drift off Solomon Islands. The round 1-seeded drupe of *Donax arundastrum*, of the Malay region, is probably water-dispersed, as it habitually grows in streams and rivers, chiefly tidal, from Burma, through Siam and the Malay Peninsula to Borneo.

AMARYLLIDACEAE.

Many of the river-bank *Crinums* have seed adapted for water-dispersal. I have given a full account of these, however, under Sea-Dispersal, p. 317.

IRIDACEAE.

The seeds of some species of *Iris* float readily for a long time. Those that float belong to the riverside species, while those that sink belong, as a rule, to inland species. Their buoyancy is due to the outer testa, which may be corky or thin and almost membranous. When this is removed, the seeds sink at once.

In species with pulpy testa, red in *I. foetidissima*, white in *I. graminea*, the seeds sink at once. These plants are bird-dispersed.

I. pseudacorus, the yellow Flag, is an inhabitant of marsh and stream. Its angled seeds have a rather thin testa of a light reddish-brown colour. They drop out of the capsule in the autumn and, when falling into water, drift away. They float through the winter till March, about 7 months. By this time the testa has become decayed and black. If this is rubbed off, the seeds sink at once. Before the end of March the testa has quite decayed away, and all the seeds are sunk. Praeger gives the floating period of the seeds as 3½ weeks. Guppy gives it as over 12 months, and he also mentions a case of seeds of this plant floating for over 2 years and then germinating while floating. Dymes also records its seeds sinking, germinating, and floating again. A number of the other species of this genus possess floating seeds. I have tested all the seeds I could get of different species in cultivation, and find that some float readily and apparently often for long periods. Those with pulpy testa, *Iris foetidissima*, etc., have no buoyancy; *I. xiphion*, the Spanish Iris, has seeds with a moderately thick, dry, but not fleshy, outer coat. They float, when dry, for a short time, but sink when thoroughly wetted.

The best floaters I have met with are the seeds of *Iris versicolor*, of North America, whose angled seeds have a thick corky testa 1 mm. in thickness, and are of a light brown colour. When the outer coat is removed, they sink at once. *I. sibirica*, which seems to be a waterside species, also possesses seeds with a corky testa which float well. It is widely distributed over temperate Asia and a great part of Europe. The similar seeds of *I. laevigata*, of north temperate Asia, Mongolia, China and Japan, are also buoyant, and those of *I. pseudacorus* are as described above.

LILIACEAE.

Being mostly inland plants, few of these have buoyant seeds or fruits. Guppy mentions the fruits of *Dianella odorata* as floating for a few days. This, however, does not appear to be a riparian plant, and the fruits and seeds are eaten by birds.

Fritillaria meleagris, the Snake's-head Lily of the water-meadows of the Thames and other rivers, is, however, certainly water-dispersed. The single capsule stands erect on the developed peduncle of the plant, whose leaves have withered away by the time the seeds are ripe. It dehisces, as do most *Liliums*, at the apex, into 3 lobes. The seeds are very thin and flat, pale fawn colour, and 6 mm. long, cuneate in outline, rounded at the outer edge, and acute at the inner tip. The testa is very thin and of loose cellular tissue, and forms a thin edge round the embryo, about 1 mm. wide. When the capsule is shaken, the seeds fly for some distance, fluttering to the ground, as do those of *Lilium* and *Gladiolus*, but in addition to this they float for months (Guppy). The fruit is ripe in June (June 3rd), and when the water-meadows are flooded later in the year, the seeds can be drifted down the river or spread further over the water-meadows. Their buoyancy is due to the thin edge of the testa, for when I removed that, the seed itself sank. The plant has been collected in Oeland (Sweden) by Palmgren, " A small island of the sea," to which it had probably been floated across the water. Some other species of *Fritillaria* and *Tulipa* have seeds which float for a short time—a day or two. They are flat and thin, the testa being rather more stiff and coriaceous, and often narrower in proportion to the seed. They absorb water soon and so eventually sink. Thus *Fritillaria askabadensis* has rather long oblong seeds, of which the testa absorbs water in a day or two. This plant, like most of the *Fritillarias*, inhabits dry, open mountain country, and is only adventitiously

buoyant, for the seeds are dispersed by wind only The same applies to the Tulips, which are pasture or open hillside plants. In some species of Fritillary and Tulip the seeds are hardly winged at all, but more or less flattened, enough to allow them to be blown by wind to some distance from the plant, the stem of which, in dwarf plants, elongates in fruit so as to allow of play in the wind; but as the dry stem is liable to fall in fruiting, the seeds are often thrown out in a pile, and then dispersed by rain-wash.

F. meleagris is the only species I can find which inhabits flooded spots and which has seeds specially adapted for flotation. It is the most widely distributed species in Europe.

PALMAE.

The fruits of very few Palms (with the exception of *Cocos nucifera* and *Nipa fruticans*, described under Sea-Dispersal) derive any great advantage from water-dispersal. Troup mentions the washing downhill by rain of the fruits of *Corypha umbraculifera* in India, and says that in the case of *Areca Catechu* (the Betel-nut), "in alluvial flats, water is an important agency in dis-" semination." I also have found Betel-nuts in the fibrous husk, washed down rivers. Guppy states that the fruits of *Pritchardia Gaudichaudii*, of Hawaii, float for 5 or 6 weeks, but those of *P. pacifica*, of Fiji, are non-buoyant. The fruits of *Manicaria saccifera* are very buoyant, and are drifted down the estuaries of the large rivers of eastern South America far out to sea. They, however, perish in sea-water, and have not been spread further than from one estuary to another. Guppy, who examined many fruits drifted up on the West Indian island beaches, remarks that on Turk's Island only 1 or 2 seeds per cent. appeared to be germinable. These Palms, he says, play the part of the Asiatic Nipa in the New World, but they have not, however, the durability of vitality in the sea that is possessed by the Nipa Palm, which, by its fibrous outer coat, is better adapted for sea-dispersal.

Mauritia flexuosa.—Sir E. Im Thurn says of this Palm (in "Among the Indians in Guiana," p. 28):—"The most common of the local Palms is the "Aeta (*Mauritia flexuosa*). It occasionally grows singly at the riverside, the "seeds having probably been placed there by the current."

Many of the Brazilian Palms inhabit the river banks of the Amazons and other streams, and are probably dispersed by the currents also.

PHILYDRACEAE.

Philydrum lanuginosum.—This plant grows in shallow sandy pools. It possesses a tall spike of capsular fruits which contain numerous minute seeds of the shape of an oblong vase narrowed to a blunt end at both extremities, and covered by short, scattered blunt processes (Pl. XII, fig. 16). The seeds float to the shallow edges of the ponds and are anchored by the processes. It is a native of Australia and the Malay region. It is very probable that it has been so widely dispersed by the seeds in the shallow waters becoming attached to the feet of birds.

JUNCACEAE.

It is somewhat remarkable that in such widely distributed and abundant swamp and riparian plants as *Juncus* and *Luzula*, the seeds of hardly any possess any buoyancy at all. The seeds of the littoral *Juncus acutus* are said (by Praeger) to float for 1½ days, and those of *Luzula multiflora* for 2½ days. In the rest of the British species, and in such exotic ones as I have tested, the seeds all sink at once.

That water plays an important part in the dissemination of *Junci* is plainly visible in any marshy field where *Juncus effusus* may be seen fringing the streamlets and often growing on river banks. In some cases the sunken seed may be washed up with silt on the sides of the streams, but their chief way of spreading is by the floating of the seedlings. The seeds sink to the bottom, germinate soon, and the seedlings float.

Rostkovia.—Of these Rushes, inhabiting the Magellan Strait, Birger (in " Du Végétation de Port Stanley ") records that of 100 seeds of *Rostkovia magellanica*, 92 floated for 30 days, and of *Marsippospermum* sp. (now included under the genus *Rostkovia*), 10 floated for 2 days. The former plant has a thick testa to the seeds, the latter a thinner one with an appendage like those of *Luzula*.

PONTEDERIACEAE.

These are all aquatic or riparian plants, chiefly tropical. The best known as a water-dispersed plant is *Eichornia crassipes*, which owes its wide distribution and present abundance to its floating shoots, described on p. 178. Petch (*Ann. Bot. Gard., Perad.*, viii, 24, p. 230) says the seeds sink in water. If allowed to dry for 1 or 2 days in the sun, and then given water, they germinate, but they do not do so under water. In Pernambuco, Brazil, where I have seen this plant in the water-meadows, the water on the fields rises and falls according to the rainfall, so that if the seeds are shed and sunk, and the water goes down so as to expose them to the sun, and they become dry in the dry season, they would germinate when the rain falls, and be washed about as seedlings.

Pontederia cordata, the Pickerel Weed of North America, has a long spike of drupaceous fruits borne on a long peduncle. When the fruits ripen, the stem reflexes from the weight, and eventually they are lowered into the water and, becoming detached, float away. The fruit is 6-angled, about ½ inch long, fleshy and green. There are raised processes in the angles which may serve to anchor it in the mud at shallow spots. They float for about a week or more, when the fleshy pericarp becomes water-logged and they sink. The pericarp decays and splits, and the seedling pushes its way out and commences to grow in the shallows. The floating period is quite long enough for the fruit to travel a considerable distance. The seedling is not buoyant.

JUNCAGINEAE.

Triglochin.—The seeds of these freshwater and salt mud marsh plants have but little buoyancy. Those of *T. maritimum* (according to Praeger) float for 4½ days, those of *T. palustre* for 6 days. Guppy says that the seeds of the two species germinate both in fresh water and sea-water, the liberated seedlings thriving afloat and producing the plumule.

Scheuchzeria palustris.—This plant grows in deep wet *Sphagnum*, in bogs full of water. In Britain it is now a scarce plant and rarely flowers. The seeds (which Guppy says float several months) might easily be drifted over the marshy moors in floods. Ravn states that the testa of the seed consists of aeriferous tissue with intercellular spaces.

ALISMACEAE.

Alisma plantago is a riverside and canal plant with a large loose panicle of many flowers producing a circle of flat rounded achenes, which are very light and are blown into the water when ripe, or the whole panicle falls so that

the achenes, which are very numerous, float away. They drift along the river until by the fall of the water they are stranded on the land. They float for from 6 to 12 months (Guppy), and 15 months or more (Praeger). I have seen them sink after 6 months. They are wide and possess a keel of parchment-like texture. The sub-epidermic cells possess an aeriferous tissue which eventually decays in the water, when the seed sinks. These achenes are also dispersed by attachment to the plumage and feet of water-fowl. The plant occurs all over Europe, temperate Asia, North America, Australia and New Zealand.

Sagittaria sagittifolia.—In this plant the carpels (achenes) have larger distinct wings of aeriferous tissue, and a large-celled light epidermis. It is due to the large size of the wings compared with the small seed that they float (Ravn). After falling into the water these wings eventually become destroyed by decay, and the seed sinks. When unripe the fruits become wet with difficulty, but when the oil in them is dissolved out by alcohol, they easily become wetted. This, no doubt, prevents young carpels being injured by water. Ripe carpels are easily wetted (Ravn). Guppy says they float for from 6 to 12 months.

Lophiocarpus guyanensis, often referred to *Sagittaria*, has even bigger-winged achenes. It is widely distributed in the tropics of both worlds.

Echinodorus (*Alisma*) *ranunculoides*, and *Elisma* (*Alisma*) *natans* have non-buoyant achenes, and the seeds of *Damasonium alisma* are also non-buoyant. The parchment wings of *Alisma* and *Sagittaria* are absent in these plants, which are more of pond and lake habitat than of moving water, but in *E. ranunculoides* the fruits, when sunk, germinate, and the seedlings float.

BUTOMACEAE.

Butomus umbellatus.—The seeds of this river-bank plant do not float at all (Guppy). By its rather sporadic habit on river edges, however, I judge that somehow it must be water-dispersed. It grows actually in the water, like *Cladium mariscus*, and the tall stem, when in fruit, falls into the water and the minute seeds escape on dehiscence of the carpels. Seeds I obtained from plants at Kew floated for a day, and then all sank. Mr. Dymes has given me notes as to some experiments he made on this plant.

Experiment I.—Seeds from Kew, September 10th, 1916. In fresh water with no mud at the bottom of the jar. Some sank September 11th, watered with a fine rose; all sank September 12th.

More seeds in another jar with mud, protected from rain, September 16th. No seeds had sunk; a mycelium was investing the testa, September 20th. All seeds floating, with much fruiting mycelium, September 27th. Mycelium-laden ones begin to sink, 4 at the bottom, September 29th. Many more seeds sink and the mycelium is off the testa, October 6th. After once sinking I have not found that any have risen again to the surface.

Experiment II.—Seeds sunk in a jar without mud, out of doors. Every now and then air-bubbles appear on the testa, and the seeds float to the surface. One seed on the surface in the morning sank again by evening, September 29th, 1916. This may be due to the fall of a raindrop on it. All seeds now sunk of their own accord were brought indoors, October 6th, and 2 seeds germinated October 19th, but no more till spring, 1917.

Experiment III.—Seeds from Kew, September 10th, 1916, 78, which had been kept dry in a packet for 28 days, floated and could not be made to sink. The bulk remained floating for 3 days. There were only 30 left floating on October 13th, and then all sank when the surface was watered by a rose water-can. None rose again or germinated till the spring of 1917.

For an aquatic plant of this nature that adaptation for dispersal seems very inadequate. The seeds will certainly float for 1 day after falling, and apparently, if quite dry, for about 5 days. If they become invested by mycelium, they may float for a fortnight. They may be disseminated by simply drifting along the bottom of the river in silt, or the seedlings may float in the spring. The plant grows in too deep water for its seeds to be dispersed by adhesion to the feet of birds in mud, and I have no reason to suppose that it is dispersed by floating clumps or rhizomes.

NAIADACEAE.

Potamogeton.—This world-wide genus, scarce only in the tropics, is largely dispersed by floating portions of the plant, and also by adhesion of fragments or fruits to water-fowl (*see also* p. 539). The floating powers of the small fruits are, on the whole, somewhat extensive. Those of *Potamogeton natans* are given as floating 12 months (Guppy), of *P. polygonifolius* (*P. oblongus*) 1½ days (Praeger), from 6 to 12 months (Guppy), *P. perfoliatus* for several months (Guppy). *P. lucens*.—I observed the fruits of this in a tank at Kew Gardens floating from September to March, the last fruits sinking in the early part of that month, so that some fruits floated for 6 months.

Fruits of *P. interruptus* (*P. flabellatus*) and *P. filiformis* float for 2½ days, *P. coloratus* and *P. alpinus* for 1½ days, and *P. pusillus* for 1 day, according to Praeger, who gives no *Potamogeton* fruit as floating for more than 2½ days.

It is noticeable that the longest floaters are the fruits of the commonest species. The fruits of *P. natans* have intercellular spaces in them (Ravn).

Ruppia rostellata.—The fruits of this plant float but a day (Praeger), but fragments of the plant bearing fruit certainly float longer than this. It is a world-wide plant, apparently mainly dispersed by attachment to water-fowl.

Aponogeton distachyum.—In this often cultivated aquatic from South Africa the seeds, 3 or more in a capsule, are emitted after dehiscence in June, and float on the water. They are linear cylindric, and about 5 mm. long. The outer testa is fleshy, green, of fine cells arranged in lines. The seed beneath is harder and brown, narrow acuminate. When the outer green testa is removed, they sink at once. Obviously, then, they can float till the soft fleshy herbaceous outer coat decays, when they sink, very much as in *Pontederia*. Marloth says (Trans. Afr. Phil. Soc., viii, p. 80) that in Africa the seed floats and germinates on the water, and gradually forms a bulb, after which the seedling sinks. J. C. Verdoorn (*S. Afr. Journ. Nat. Hist.*, iii, 19) says that after floating 8 days the testa splits and the seed sinks and germinates in the mud; but in one case the seed was unable to escape from the testa, and it germinated on the surface of the water. We have here an excellent example of the floating seed, prevented from floating too far (to an unsuitable situation) by its buoyant testa (after a period sufficiently long to allow it to be carried a considerable distance by river current) dehiscing and releasing the seedling, now too heavy to float.

TYPHACEAE.

Typha.—These plants are naturally wind-dispersed, having very light plumed fruits. According to Praeger, however, the fruits of *Typha latifolia* float for 4 days, those of *T. angustifolia* for 4 weeks, and Birger has found those of *T. latifolia* floating in drift off Tjuron Island, Sweden. The buoyancy of these fruits may be useful to the plants as allowing those which fall in the water to drift on to mud-banks, where they could grow.

Sparganium.—The fruits of all the Bur-reeds are adapted for water-dispersal, though they are also dispersed through being swallowed by ducks. They

inhabit river and canal banks, growing in the shallow edges. The fruits owe their buoyancy to the thick corky pericarp, the endocarp woody, the epicarp spongy. They are about ¼ inch long. Those of *S. ramosum* are rather thick, fusiform, those of other species more slender. The fruits of *S. ramosum* float for 12 months, of *S. minimum* and *S. simplex* 6 months (Guppy), over 15 months (Praeger). Guppy has seen drupes of *S. ramosum* floating and germinating after 2 years, and kept some in sound condition floating for 4 years. The species are widely spread over the north temperate region, and some also occur in Australia.

ARACEAE.

In most of the Aroids the seeds are dispersed by birds, but some are water-dispersed, and especially those which inhabit the banks of streams, rivers, and marshes. Seeds of *Arum maculatum* and such bird-disseminated plants usually sink at once in water.

In *Calla palustris*, a creeping Aroid of the marshes of Europe and temperate Asia, the fruits are pulpy and red, forming a dense spike about 3 inches long. They are greedily eaten by ducks, which also swallow the seeds. When the fruit is not eaten, but decays of itself, the seeds float out and lie horizontally in the water. They are small and oblong, blunt at both ends, and a very light grey colour, with a prominent brown raphe. They are faintly ribbed at the base with transverse bars, the spaces between which, in the upper part, form pits. The testa of the seed consists of aeriferous tissue with intercellular spaces (according to Ravn). They float for 12 months (Guppy).

In the Malayan region we have a stream-bank genus of Aroids, *Piptospatha*, which grows in cracks of rocks in streams. It is allied to the genus *Schismatoglottis*, which in turn is allied to *Homalomena*. This latter has a large limb to the spathe, which is persistent till the fruit ripens. The plants are fertilised by beetles, which are rather scarce in Malay forests. Hence the evolution of *Schismatoglottis*, in which the spathe limb falls off when the flowers open, so that the spadix is exposed to the wind, and the pollen, blown away in abundance, fertilises other plants, thus this genus is anemophilous. In these Aroids, as well as many others (*Colocasia gigantea*, etc.), the seeds are simply dispersed by rain-wash. *Piptospatha* is practically a *Schismatoglottis* somewhat adapted for stream-dispersal. The limb of the spathe falls off, and the base forms an open obconic cup in which the fruits lie more or less loose and can be washed away by the rush of the torrent, and deposited in cracks in the adjacent rocks.

Cyrtosperma lasioides is a tall marsh plant of the Malay region. The large spikes of fruits are not very conspicuous, and are not, so far as I know, eaten by birds. The seeds are rather large, horse-shoe-shaped, with a strong toothed crest, and similar seeds occur in the African *C. senegalense* (Pl. XII, fig. 20). There can be little doubt that these plants are water-dispersed, the papillae or teeth on the crest serving to attach or anchor them to the mud. The allied genus *Podolasia*, an inhabitant of dry forest, has quite smooth seeds.

Orontium aquaticum.—An aquatic Aroid of North America inhabiting ponds, ditches and rivers. The peduncle of the fruiting spike is so deflexed as to be submerged in the water. The fruits, about ½ inch long, are green and fleshy, obovoid. They float readily in the water, being detached from the spike when ripe. The pericarp is moderately thick, the single round seed has a viscid slimy dark green testa, and is about ¼ inch through, globose, with the plumule at the top. There is a hole or pit in the centre of the seed towards the base, but this appears to have no importance as a cause of buoyancy, as the seed sinks at once on removal of the pericarp, which floats when detached. The

floating fruits sink in a week, the pericarp becoming water-logged. After another week the pericarp decays and, opening at the apex, releases the seed, which immediately germinates (Pl. XII, fig. 6).

In *Cryptocoryne*, *Typhonodorum* and *Aglaodorum* there is a very different system, and a peculiar structure and evolution of the seed adopted. The plants, in fact, are viviparous, and the primitive foliage and radicle are developed to some extent before the seed escapes from the ovary. In *Cryptocoryne*, only the history of *C. ciliaris*, a tidal swamp and river plant, has been described. Most of the species are inhabitants of streams in the Indo-Malayan region, and possess submerged spathes, only the tops of which appear above the surface of the water, the leaves also floating on the top like those of a Water-lily. The peduncle continues to grow after fertilisation, till the ovaries project above the water, for during the flowering stage the female portion of the spadix is under water. In some specimens, however, the spathe is not always, or entirely, submerged.

C. ciliaris is a tidal-mud plant with creeping rhizomes and stiff erect leaves, inhabiting the tidal rivers of India and Malaya, from Bengal to the Malay Peninsula, Borneo and Java. The fruit is a conic capsule 1 inch through, containing from 6 to 8 seeds. When ripe, it dehisces and discharges the seeds in the water. They are very small, and when released possess a plumule of numerous dark-green linear filaments, at the base of which is the radicle. Below this is a small oblong body, the cotyledon. A few minutes after the seed is released this body becomes detached, and the upper part, the plantlet, floats away, to be later stranded on the mud on a falling tide, when it then commences to grow. Good descriptions of this evolution are given by Griffith (in Trans. Linn. Soc., xx, 12), with figures, and by Goebel (in "Morphologische und Biologische bemerkungen Flora," 87, 1897, p. 426). A somewhat similar principle is adopted by *Aglaodorum Griffithii* (*Aglaonema palustre*), another tidal-mud creeping Aroid of very similar habit to that of the *Cryptocoryne ciliaris*, and actually growing with it in the tidal rivers of the Malay Peninsula, Sumatra and Borneo. The rhizome creeps beneath the mud, throwing up large leathery ovate leaves, and spikes of large green ovoid fruits, 1½ inch long and 1 inch through, with a thick pericarp, which floats readily. Each ovary contains but 1 seed, from the top of which, before it is freed from the pericarp, project 5 fleshy linear leaves at the base of which emerges a stout root. The upper part of the seed is green and fleshy, but the basal portion, which is separated by an indented line, is brown and rather corky. This organ, I suppose, corresponds to the basal mass in *Cryptocoryne*, believed to be the cotyledon. This plant has often been referred to the genus *Aglaonema*, a forest genus of Malayan plants, in which the fruit has a brilliant red pericarp, and is dispersed doubtless by birds. *Aglaodorum* is adapted for river-dispersal, and the seed is nearly the largest of any species in the order (Pl. XII, figs. 11 and 12).

Typhonodorum Lindleyanum.—This extraordinary plant inhabits rivers and ponds in Madagascar and Zanzibar, and, as the fruits are eaten by natives, has also been transported to other islands in the Mascarene Archipelago. It has a tall, stout fleshy stem 6 feet or more in height, and large petiolate ovate cordate leaves. The fruits, as in *Aglaodorum*, are 1-seeded. The seed is from 1½ to 2 inches long, obovoid flattened. The plumule projects at the top and lies curved over the apex, below it is the embryo, and the greater part of the seed, below which is a round, flattened, apparently corky mass, the albumen. At the base of this is a small round body called the haustorium, which, I presume, corresponds to the large, corky brown mass at the base of the seed in *Aglaodorum*. The pericarp is thinner than in the latter plant, is more pulpy, and soon decays. The seed is floated clearly from the corky albumen, and as

long as the "haustorium" persists, the seeds float erect, but when that is detached, it floats on its side.

I am much indebted to Mr. A. W. Hill, the Director of Kew Gardens, for information and specimens of this remarkable plant, which is successfully cultivated at Kew, and of the germination of which he has been making a special study.

All these three aquatic Aroids, belonging to totally different affinities, appear to have evolved, independently, much the same methods suitable for dissemination. They are viviparous, the seed germinating on the plant. They possess a floating body formed apparently of the albumen and cotyledon of the seed, of which all, or a portion, is detached during floating, so that the young plant may be stranded eventually on the mud.

I have put these three Aroids together under River-Dispersal on account of the similarity of the two saline marsh inhabitants to the freshwater *Typhonodorum*. These *Cryptocoryne ciliaris* and *Aglaodorum* have spread evidently by sea to some distance along the Indo-Malayan coasts, but both perhaps as much by floating pieces of the rhizome as by seedlings. They have not, however, been as successful in distribution as the marine seedlings of *Rhizophoraceae* or *Avicennia*.

Acorus calamus, another aquatic and riparian Aroid, is now mainly dispersed by its rhizome floating away in floods. It very seldom fruits.

LEMNACEAE.

The Lemnas owe their wide distribution to the transport of the whole plant by floods or rivers, or adhesion to birds or batrachians, and are treated of under those sections. They seem to produce seed but rarely. Ravn states that the testa of the seed consists entirely of aeriferous tissue with intercellular spaces, as is the case in those of *Menyanthes* and *Scheuzeria*, so that they may be dispersed also by their floating seeds, occasionally at any rate.

ERIOCAULACEAE.

H. Lecomte (in "Dissémination des fruits et graines chez les Eriocaulonées," *Journ. de Bot., Paris*, 1908, p. 129, with figures) gives an account of modifications in *Eriocaulons* which are destined to give their seeds floating powers.

The *Eriocaulons* are grass-like plants in which the minute flowers are clustered into a head at the end of a peduncle, after the manner of a Composite, and, as in these, the head is surrounded with an involucre of bracts. The genus is very widely distributed over the world, the greatest number occurring in South America, where in open heathy country they are very abundant. One species is found in Ireland and Western Scotland, and also North America. A few occur in Africa, a considerable number in tropical Asia, and some in Australia. They are scarce in temperate climates, and absent from Polynesia and most of the smaller islands of the world. Most of the Old World species inhabit very wet spots, lakes, rice-fields or margins of streams, while many of those of the New World inhabit heathy dry regions, where some of them form moderately large branched trees.

The flowers in the heads are unisexual and possess 1 or more bracts, 3 sepals and 3 petals. The petals usually have white filamentous hairs, and in some species, where they persist after flowering, the fluffy petals act as wings for fruit dispersal. The female flower has an ovary of 3 lobes, each lobe containing a single seed released by dehiscence. The seeds, which are very minute, are usually striate or papillose.

In many cases the seeds, I have reason to believe, are dispersed by attachment in mud to the feet of wading birds.

In most, however, the seeds are dispersed by rain-wash or streams, the striae or papillae acting as anchors to retain the seeds on the mud and prevent their being washed away into deep water, as is common in plants growing on muddy stream-edges. The little Malay *Eriocaulon truncatum* haunts the runnels by paths and such-like spots, where the seeds are carried along and retained in roughnesses of the mud, where they can germinate.

Lecomte found in Cambodia two species inhabiting the deeper water of rice-fields which have strange modifications for floating the seeds fallen into the water.

He commences his article by pointing out as a parallel the dispersal methods of rice. The ripe grains of this semi-aquatic are enclosed in the two hardened glumes, which form a kind of box to contain it, the inner glume being furnished with a short awn, the outer one with a longer one. The outer and lower glume forms a boat-like organ, in which the rice grain can float away till it reaches a suitable mud spot in which to germinate.

In *Eriocaulon*, he says, the seeds are covered with short villosities arranged regularly to prevent the seed from sinking to the bottom of the water. They may have this effect, but I am more inclined to the view that these villosities, or papillae, play a more important part in causing the seed to be arrested when in contact with the mud.

The petals in the species he has examined are villous, and when the 3-lobed fruit is detached, they come away with it, and, being situated in the grooves between the lobes, they serve to prevent the ovary cells from dehiscing and letting out the seeds, and also play a part in floating the fruit and allowing of further dispersal.

In *E. alatum*, of Indo-China, a rice-field plant, there are only 2 sepals, and these are boat-shaped and enclose the carpels, and have on the back a prominent crest or wing, denticulate at the upper edge. This wing serves to float the carpel containing the seed, or may act as a wind-dispersal wing. The whole fruit breaks off when ripe, and when it is drifted to an elevated spot in the rice-field, where these plants grow, it dries, the outside of the calyx contracts more rapidly than the inside, the two edges of the concavity separate and let out the carpels, which then dehisce.

In *E. guianense*, of Cayenne, the sepals of the female flower are somewhat similar to those of *E. alatum*, possessing a broad wing, but the sepals of the male are not boat-shaped or winged, being simply ovate and apparently flat.

In *E. longifolium* and *E. sexangulare*, of Indo-Malaya, both male and female flowers have boat-shaped sepals with wings, but the female sepals are deeper and more concave, and the wings are of a spongy texture.

It is clear that these boat-shaped sepals are derived from a simple ovate sepal, as is common in *Eriocaulon*, incurved round the ovary, probably from pressure of the other flowers in the head, and becoming stiffened, and the keel is an outgrowth of the central vein of the sepal.

Another remarkable modification described by Lecomte occurs in *E. nautiliforme*, also collected by him in Indo-China. In this species the female flower has a bract as big as the flower, and 3 sepals, one of which is convex and rounded, rather warty on the back, and somewhat of the shape of a nautilus shell. It is stalked below, and the 3-lobed ovary is also stalked. The shell-shaped sepal encloses one of the lobes (carpels) of the ovary, and when ripe it breaks off, carrying with it the whole ovary, which thus floats away in the sepaline boat.

In another form from a different locality the shell-like sepal is less curved and has a short terminal point.

In *E. Lamarckii*, of Africa, and probably the same species as the type

collected in Guiana, the female flowers have 3 erect sepals joined at the base so as to form a circle round the rest of the flower. When the seeds are ripe the sepals, at first erect, become dry and recurve, and by pressing against the other flowers in the heads, force themselves out, carrying the capsule with them.

The *Eriocaulons* are strictly continental plants; they do not appear to occur in any remote islands, and are mostly tropical. In Brazil, where they are very abundant, many species inhabit dry sandy spots where water-dispersal can hardly be effective, so that these species are probably disseminated partly by wind, partly by rain-wash.

CYPERACEAE.

Many of the Sedges are inhabitants of marshes and riparian localities, but, though widely distributed throughout the world, the achenes or nuts seem rarely to possess any buoyancy or any special adaptation for floating.

A small number are sea-dispersed and are treated of under that section, and rain-wash certainly plays a considerable part in their local dispersal, but actual floating on rivers is comparatively scarce.

The nuts of the *Cyperi* (Clarke says) usually sink at once in water, but there are several species of one section which are distinctly modified for dispersal by streams and rivers. This is the section *Anosporum*, of which the species inhabit pools, rivers, rice-fields, etc., in the open country of Africa and India.

Cyperus (*Anosporum*) *cephalotes* is a floating Sedge, abundant in India and also found in Ceylon, Burma, Amoy, Borneo, Java, and Australia. In some of these countries the seeds may have been imported in rice and, being sown with it, it has thus established itself. It appears to be quite a recent introduction into Australia. The nut (unlike most other nuts in *Cyperus*) is supported on a short pedicel, which, when ripe, forms a thick, spongy corky base to the nut, dilated into short wings on either side by which it can float. A good figure of it is given by Clarke (Journ. Linn. Soc., xxi, pl. I). *C. nudicaulis* and *C. colymbetes*, of tropical Africa, resemble it. These are sudd plants and form part of the great floating mass of vegetation in the big rivers of Africa.

C. cephalotes is an inhabitant of rice-fields and pools in India, and, according to Clarke, the roots are entangled in a mass of rotten *Pistia* and *Salvinia*, so that the rhizomes and clumps of the plant may perhaps be dispersed by river in these floating masses of decayed vegetation.

Cyperus platystylis grows with *C. cephalotes* in this way, though its nuts are not provided with the floating apparatus of the latter species, but have corky edges. It is spread from India to Australia, largely, I believe, in rice-grain. It only occurs in rice-fields in the Malay Peninsula.

Carex.—Most of the *Carices* are more or less dispersed by water from the buoyancy of their utricles, which, containing air, float, carrying the nuts enclosed in them. The genus is very widely distributed, and many of the species, including some which have good floating powers, are inland plants, e.g., *C. panicea*, *C. stellulata*, and *C. flava*, and can very rarely come into contact with moving water, unless it be occasional floods. The following data are the periods of flotation given by Praeger and Guppy, with notes from Birger:—

12 months and over .. *C. dioica*, *C. paradoxa*, *C. canescens* (also found floating in drift off Tjuron Island by Birger), *C. acuta*, *C. aquatilis*, *C. panicea*, *C. vulpina* (this latter species occurs along the Thames bank and on silt banks near Barnes, evidently brought down by river), *C. flava*, *C. riparia*, *C. diandra*.

12 months	..	*C. pseudocyperus* (Praeger); 6 months only (Guppy); *C. stellulata*, *C. remota*, *C. paniculata* (Guppy).
9 months	..	*C. elata*, *C. stricta* (Praeger).
5 months	..	*C. rostrata*, *C. ampullacea* (Praeger).
4½ months	..	*C. limosa* (Praeger).
Several months		*C. leporina* (Guppy).
1½ months	..	*C. vesicaria* (Praeger).
From 2½ to 3 weeks	..	*C. flacca*, *C. Hornschuchiana*.
1½ weeks	..	*C. extensa*, *C. helodes*.
Under a week :—		
5 days	..	*C. fusca*.
3 days	..	*C. pallescens*, *C. divulsa*.
2½ days	..	*C. pilulifera* (an inland plant).

Fruits of *C. Goodenovii* (*C. vulgaris*) were also found floating in the drift of Tjuron Island by Birger.

None of the species examined and recorded were found to be actually non-buoyant, except the utricles of *C. distans* and *C. hirta*, both of which inhabit wet marshy districts. Most of the riparian species have utricles which float for over 6 months. The genus is absolutely world-wide and very abundant. It is mainly continental, but 2 endemic species occur in Tristan d'Acunha, 2 in St. Helena, 1 in the Bermudas, and 1 in Juan Fernandez and Masafuera. In the tropical oceanic islands there are none, but in the tropics these plants are mostly mountain plants. Guppy has a long article on the distribution of the genus in "Plants, Seeds and Currents," and points out the importance of birds treading on the utricles and carrying them away on their feet, and in view of the occurrence of species in the Atlantic islands, this seems the most probable reason for their presence there. Over continents, however, they appear to be largely diffused by floods and rivers.

Blysmus rufus.—The fruits of this (according to Ravn) have no air-tissue, but (Praeger says) they float for a week, Guppy from 1 to 6 months. The fruits are dispersed by floods over the salt marshes it inhabits. *B. compressus* has an air-tissue like that of *Alisma* (according to Ravn). It is a marsh and stream-edge plant. The bristles surrounding the nut are persistent and barbed, and possibly serve as adhesive organs. In *B. rufus* these bristles are nearly suppressed. There is no record as to whether the nuts of *B. compressus* float.

Scirpus maritimus.—The nuts of this plant float for at least a month. According to Ravn, the buoyancy is due to the pericarp. When this decays the nut sinks. The plant migrates up tidal rivers, as at Kew, and is also dispersed by water and sea-fowl. I have more fully described it under Bird-Dispersed Plants (*see* p. 548). The nuts of *S. Tabernaemontani*, a river plant growing with *S. lacustris*, float 1½ days (according to Praeger). The nuts of the very widely distributed *S. lacustris* and other species of the genus do not float for more than a few hours, or not at all, except *S. Savii* (*S. filiformis*), which, Praeger says, will float for a day. None of the genus *Heleocharis* are recorded as having floating nuts. That all of these are dispersed by water one can have no doubt, but this is either effected by the drifting of portions of the rhizomes, or by the seeds being rolled along in silt. (For migration by rhizome, *see under* Dispersal by Vegetative Portions, p. 183)

Of other *Cyperaceae* we have *Cladium mariscus*, a very widely dispersed marsh and river plant, of which the oval nuts float (according to Praeger) for 15 months or more. It probably owes its actual wide distribution to the attachment of

its nuts to the feet of wading birds, but in places where it is very abundant, as in the Norfolk Broads, its local distribution is no doubt due to its floating nuts. Ravn states that its nuts have dry flesh composed of air-cells with thin walls and large intercellular spaces. The seeds sink readily if the flesh is removed. Similar structures occur in the nutlets of *Mentha aquatica* and *Sparganium*, and much resembling the fruit of the latter is the nutlet of the tropical Sedge *Scirpodendron*, not rare in tidal swamps in tropical Asia. This plant grows in water, like *Cladium*, and its nuts readily float away when the water rises. Largely, however, they are carried off by rats, which eat the corky exterior.

Schoenus nigricans is chiefly a wet or sandy heath plant. According to Praeger, its nuts float for 2 days, and those of *Rhynchospora fusca* 2½ days.

Considering how many of these *Cyperaceae* grow in wet spots, it is very remarkable how few of them owe anything to river or flood-dispersal, and yet how very widespread they are.

GRAMINEAE.

Water plays but a small part in the dispersal of grasses except in the life-histories of the littoral and riparian species. Some of these are disseminated by the aid of the glumes or bracts containing the grain, and acting as boats, as in *Coix*, *Thuarea*, *Digraphis*, *Leersia*, *Oryza*, etc., as described under Bracts (p. 194), and some species are largely dispersed by floating rhizomes or tufts of grass, both by river and sea, as in *Spartina*, *Saccharum*, *Phragmites*, etc. *See under* Dispersal by Water of Vegetative Portions, p. 182.

Praeger gives a long list of British grasses of which he has tested the buoyancy, but the only ones he records as floating for a week or more are the grains of *Setaria viridis* and *S. glauca* for 1½ and 2½ weeks respectively, and *Festuca fasciculata* and *Sclerochloa loliacea* 3½ weeks. Of all the rest of the species he gives, the grains float only from 1 to 3 days, except a few riparian species. The greater part of the grasses, however, are inland plants, and not therefore likely to be water-dispersed. He does not make it clear whether he is dealing with the grain free of the glumes or not. In *Setaria* the grain is detached from the glume, while in *Festuca* the glumes fall with the grain.

Of the riparian plants he records *Digraphis arundinacea* as floating for 6 days, *Glyceria aquatica* 5 days, but *G. fluitans*, one of the first grasses to appear in a new pond, is only recorded as floating for 2½ days.

Catabrosa aquatica, also a river plant, has fruits which float for 1 day. *Lolium perenne*, which I have seen coming up in the embankment of the Thames below high-water mark, floats for 2 or 3 days. But probably these grasses owe their floating powers to their persistent glumes only, and I have already referred to this under Bracts as Floating Organs, p. 194. I doubt if any grasses are actually dispersed by the floating of the grain unassisted by the glumes or bracts.

GYMNOSPERMAE.

Gnetaceae.

Gnetum fruits have been met with in sea-drift. They are mostly forest climbers, more rarely trees and shrubs, with pink fruits, dispersed by birds, but as some at least grow by rivers, they may be spread about by water in forest areas. *G. Wrayi* has large corky fruits, 3 inches long and 1½ inch through. It grows by rivers in forest, and is probably water-dispersed.

CONIFERAE.

None of these are at all likely to derive any advantage from the little buoyancy that some possess.

Juniperus communis.—Dry berries will float for 3 or 4 weeks. *Pinus sylvestris* seeds from 1 to 4 weeks (Guppy). *Dammara vitiensis* seeds from 7 to 10 days (Guppy).

CYCADACEAE.

Cycas Rumphii, a sea-coast tree, has seeds dispersed by sea and, where any of these plants grow up rivers, the seeds may be drifted along the banks.

PART III

DISPERSAL BY SEA

Foreword—Sea-Dispersed Plants in Islands, Routes of Migration, Summary—Evolution of Sea-Dispersed Plants, Duration of Vitality in Immersed Seeds—Seeds carried by Driftwood and Pumice—Stems or Branches Dispersed by Sea—Marine Submerged Flowering Plants—Algae—List of Terrestrial Flowering Plants with Seeds Dispersed by Sea-Currents.

Foreword

The dissemination of plants by sea-currents from coast to coast and from island to island is one of the oldest forms of dispersal, though, as far as terrestrial plants are concerned, wind and air-currents served to diffuse the early plants, ferns and other cryptogams, in the more primitive times. In the mesozoic age, when *Cycadeae* and other *Gymnosperms* with heavier fruit became abundant, sea-transport naturally came into play, and was probably nearly as important then in the dispersal of plants as it is now. About fifty years ago I was standing on the edge of a coral reef of the Coral Rag-Formation (middle Oolite) in a field near Oxford, and wedged in between two ledges of the reef I found a fossil fruit of about the shape and size of an olive. It was perhaps the seed of a Cycad or allied plant, or of a Gingko tree which had drifted from a long distance, to be carried up by the waves on the coral reef and firmly wedged between the two layers, just as one may see to-day modern seeds thrown up on a coral island. In the Eocene period the fruits of the Nipa Palm were drifted about by sea in Southern Europe, as they are now in the East Indies.

Alphonse de Candolle (in his "Geographie Botanique," 1855) attributed little importance to the dispersal of the seeds of plants by sea-currents, at least for very long distances, although he allows some importance to the seeds travelling by short stages in this manner. We know now, however, that the distances seeds can travel by sea unharmed and in a fit stage for germination are the longest of any method of transport, certainly over 1,000 miles. The number of species which can travel by this system is, however, limited for two reasons. Firstly, the seeds or fruits must be able to float for a long period of time without absorbing water (and so becoming water-logged or commencing to germinate too soon), or if, as sometimes happens, they do germinate in the sea or enter it as seedlings (as the fruits of the Mangroves (*Rhizophoraceae*) do), they must be able to float as seedlings for a long period. Secondly, the seeds must be able to establish themselves when landed on a littoral soil, either a sand-bank or a shingle beach or tidal mud. That is to say, they must be able to resist the action of salt at all stages of their growth. This naturally entails that the plants so disseminated must be of species adapted to growth in sand, shingle or saline mud—in fact, they must be littoral plants.

Of the immense number of fruits and seeds carried down by the big continental rivers to the sea, all over the world, very few fulfil these two conditions, only the fruits and seeds of trees, shrubs, or herbs which grow within the saline area, at the mouths of the rivers as far as the tidal water ascends, or grow on the seashore, can survive these voyages. Many seeds of riparian plants, such as those of *Pangium*, *Hodgsonia* and *Grias*, which are regularly river-dispersed, are carried by the sea-currents to immense distances in the sea, but arrive

on the shores either dead, or, if not actually past any possibility of growth, are quite unable to establish themselves on sea-mud, sand or shingle beach.

The importance of the regularly dispersed littoral plants lies in their furnishing the first vegetation on new shores, whether island or mainland. Many are trees and shrubs, whereas most wind-borne plants are herbaceous, and it is not till the trees have grown that land birds can come and bring plants with baccate or drupaceous fruits, nor can epiphytes or shade-loving plants appear. There is also reason to believe that some of the originally littoral plants have, after settling on an island, produced inland forms by evolution.

The number of species of sea-dispersed plants is comparatively small, far smaller than the number of species dispersed by wind or birds, and far the largest number range from Polynesia along the tropical coasts of Southern Asia as far, in some cases, as East Africa.

Sea-dispersed plants are very scanty in the north temperate region, and are not abundant along the coasts of South America and West Africa.

This, I suggest, is due to the broken-up nature of the land area in tropical East Asia. The outline of the coast here is irregular, and there are innumerable islands (largely coral) lying between the furthest part of Polynesia and the Mascarene Islands.

A number of seeds and fruits which float a long time and travel to great distances come from certain parts of the world, especially South America, and drift northwards by north-flowing currents, so that they are carried far beyond their limits of climate. Such are the seeds of *Entada*, *Mucuna*, *Saccoglottis*, *Guilandina Bonduc.*, etc., which are borne to the coasts of the Azores, British Isles, Faroes and Scandinavia. Though the seeds often arrive in good condition, the climate is utterly unsuitable for their habits, and so these seeds are wasted.

The actual direction of the currents from the river mouth is one of the most important factors in the distribution of plants whose seeds are water-borne. The actual limit of distance to which sea-borne seeds can float, in a sound condition, is at present difficult to state. It undoubtedly varies largely with the species. Floating seeds in the sea may become water-logged, or perish from injuries due to boring mollusca and other causes.

There is also, among successfully sea-distributed plants, another factor to be taken into account, the habitats of the littoral species. Plants which grow on tidal mud or in tidal rivers fail if their seeds are cast up on a beach of shingle or sand, and those of a sandy beach habitat fail to make good if stranded on tidal mud.

Now, in most parts of the world, especially tropical Asia and Polynesia, tidal swamps are scarcer than sand-banks or coral beaches. Tidal mud implies a continent or large island with big or at least fair-sized rivers to bring down that class of silt which forms the characteristic blue or grey mud. Hence tidal-mud plants are absent from a large number of the smaller islands, and frequently from large tracts of coast, where big rivers are absent, e.g., Christmas and Cocos-Keeling Islands, the greater part of the east coast of the Malay Peninsula and of East Africa.

The constitution of the shores of any land depend on the geological structure of the interior. Thus the mountains of the west coast of the Malay Peninsula are of granite, with a flanking broken-up line of limestone. These wash down by denudation into a thick blue mud, suitable for the growth of Mangroves and tidal-river-mud plants, which are therefore abundant, to the exclusion of sand-hill or beach plants. On the east coast of the Peninsula the interior mountain ranges of granite are flanked outside with a range of sandstone, which washes down to form extensive sandy flats along the sea-coast, continuing as far south as to Eastern Singapore. The

littoral flora is therefore quite different from that of the west coast. Mangroves and tidal-river plants are almost entirely absent, being found only in a few rivers which have brought down and deposited mud from the interior granite hills, and the littoral flora consists of *Casuarina*, *Ipomoea biloba*, and *I. denticulata*, *Spinifex*, and such sand-loving plants.

Tidal-river fruits and seeds must be capable of floating uninjured in the sea till they come to the mouth of a tidal river, up which, with a rising tide, they can drift till they are stranded. Some can establish themselves in brackish water, but most have a limit based upon the amount of salt in the water. When they reach this limit they stop and go no farther. Thus *Scirpus carinatus*, *Sc. triqueter*, and *Sc. maritimus* grow up the Thames a hundred yards or so above Kew Bridge, where they stop, although the tide runs to Teddington, some miles further up the river, but, this water being perfectly fresh, the plants will not grow there.

Some of the tidal-river plants are very local. Probably their seeds float for a very short time successfully in open sea. Such is *Aglaodorum Griffithii*, limited to the Malay Peninsula and the islands of Borneo and Sumatra, which, there is every reason to believe, were formerly connected with the Malay Peninsula. *Sarcolobus* and *Finlaysonia* are limited to the Indian and Malay Peninsula coasts and Borneo. This class of plants seems merely to have drifted a short way along the coast, and then to have been carried up the next tidal river, and so crept along the coast. However, *Aglaodorum* and *Cryptocoryne ciliaris*, the seeds of which float for a very short time, may also have been dispersed by fragments of their stout rhizomes floating in the sea, and the *Cryptocoryne*, which grows in Nipa groves, may have had its seeds or portions of rhizome carried in the large detached clumps of *Nipa* which so frequently are to be seen drifting in the currents in Malayan seas. It has travelled as far as New Guinea, though its seeds do not float for a day.

SEA-DISPERSED PLANTS IN ISLANDS.

In the case of newly-formed islands, or islands in which the vegetation has been destroyed, sea-dispersed plants form the most important part of the first vegetation to cover the ground.

The first plants to reach an island of this nature are those dispersed by wind, but of wind-dispersed plants few can effect a lodgment on the bare soil on account of their non-resistance to the exposure and heat of the sun. With the exception of Tree Ferns, none of these plants are even shrubs. Trees and shrubs are at first only brought by sea. Until they are well grown, no shade-loving plants, climbers or epiphytes can establish themselves, nor do frugivorous birds or bats come to bring the seeds of baccate or drupaceous fruits or figs. Some islands bear only sea-transported plants for a very long period. In Diego Garcia, for instance, out of 36 species of plants collected there, 26 are sea-transported, 11 probably introduced by man, and 1 perhaps by the adhesion of its fruits to birds, and of the 11 recorded as introduced by man, possibly some of those came by sea. The wind has brought but 8 Ferns and Lycopods and 1 moss, and frugivorous birds and bats nothing.

In Cocos-Keeling, of the flora 14 are sea-borne species, 5 brought by adhesion to birds, 1 moss, and 1 fungus by wind.

In Krakatau the first expedition after the destruction of the flora found 9 sea-borne plants, 4 wind-borne Phanerogams, and 13 Ferns. Here the adjacent land of Java was only 25 miles away, so that the wind-borne plants could come more readily. All the wind-borne flowering plants were herbaceous, and most of them could not have established themselves except for the protecting

shadow of the sea-borne trees. For the more distant islands, Diego Garcia and Cocos-Keeling, it will be noticed that sea-borne plants preponderate greatly. These plants can travel further than wind-borne plants, though more slowly.

The Routes of Migration by Sea.—Guppy (in "Plants, Seeds and Currents," chap. iii) gives a map of the world showing all the main ocean currents which traverse the oceans and run along the coasts of the continents, and might transport seeds to almost any part of the land shores. But, in studying the distribution of plants by sea-currents, we find that the routes by which these have travelled are very few in comparison with the large extent of sea-currents over the globe.

From the point of dispersal of plants, the most important information that we get is derived from the occurrence of plants that we know are adapted for sea-dispersal, in distant islands, not only remote from the continents, but which we have reason to know never have been connected with the mainland, such as coral atolls and volcanic islands. Among these, very important are the coral islands of Cocos-Keeling and the islands of Christmas, the Maldives, Minikoi, Laccadives, Diego Garcia, etc. Of these, Christmas Island is of great value, as it was investigated by botanists before any settlement was made, so that any confusion due to the interference of human agency is eliminated. This great advantage is obtained from but few other islands, though we have an equal value in the island of Krakatau, in which the flora was entirely destroyed, in 1883, by a volcanic eruption, and which has been visited since by expeditions in 1886, 1897, 1906 and 1919, to investigate and catalogue the plants as they invaded the island from Java, 25 miles away, till the island, in 1919, was densely covered with vegetation.

The sea routes of the wandering seashore plants are indeed few compared with the large number of sea-currents shown by Guppy in his map, and it seems clear that some of these, however powerful, have played but a small or no part in dispersal. This is probably due mainly to the comparatively short life of seeds in the sea, for when the water penetrates to the kernel of a seed, either germination commences or the seeds decay; in either case the plant perishes. In the case of plants of which the already germinated seedlings are transported by sea, such as the *Rhizophoraceae*, *Avicennia* and *Aegiceras*, the young plant still requires to reach a safe place in which to develop within a limited time, and, besides, it is liable to injury by the roughness of the waves striking it against other floating matter, or from the attacks of marine animals—mollusca, teredo, or crabs.

The distance, however, that some of these plants can travel by sea is very great. A large number of seeds are known to have been conveyed by the Gulf Stream from the West Indies to Europe, a journey which Guppy estimates of at least a year's duration, owing to the course of the current which runs up the American coast towards Newfoundland before it turns across towards Europe. Many of these seeds appear to have arrived in Norway and on the English and Irish coasts in good condition for growing, and some from the Azores actually germinated and grew after a voyage of nearly 3,000 miles. It is noticeable that of these long-distance travellers nearly all belong to the most widely distributed genera and species of all the sea-transported plants, viz., *Mucuna*, *Guilandina*, *Entada*, *Dioclea* and *Ipomoea*.

It is not at present always easy to fix the original centre from which a plant was distributed, and this often makes it difficult to decide whether it migrated from east to west or from west to east. In some cases, however, it is quite clear, if one assumes that the migrant starts from a country where it has many relatives, and where the migrating species is connected by obvious affinity with other genera, as in the case of *Dodonaea*, *Spinifex*, *Casuarina* and *Cassytha*. Of these plants there are numerous allied but dissimilar species in Australia,

most of which are not at all adapted for sea travel, while in the more distant regions we find one sea-borne species far away from all its relatives. We may therefore conclude that the widely-spread species is derived originally from Australia. We find, however, occasionally, inland species living far away from the original home of these plants, and differing in some respects from the seashore one. Thus the seashore form of *Dodonaea viscosa* is a low sand-hill shrub, but in India, Java, and other places we find a tree very different in habit and species, with quite different foliage and even fruit in Hawaii. The *Dodonaeas* of this type, however, are able to be wind-dispersed (*see under* the section of Wind Dispersal, p. 74), and could easily be spread inland by wind, and may readily alter or become modified into the very dissimilar-looking tree form. The same thing has happened in the case of *Cassytha capillaris*, of Ceylon and Borneo, and *Colubrina pedunculata*, of Christmas Island.

Under Wind-Dispersal I have pointed out the line of evolution of *Heritiera* from *Sterculia* (*see* p. 84). The nearest ally to the seashore and inland *Heritieras* is the genus *Tarrietia*, a Malayan genus. There is no other genus at all like it elsewhere. *Heritiera* is abundant on the seashores of Malaya, and has spread along the islands for a long distance. We may safely affirm that *H. littoralis* was evolved in the Malay region, and spread by sea to East Africa westwards and to Polynesia eastwards.

In many cases, however, our knowledge of the history and migrations of some plants is not yet adequate enough to decide from whence the plant originated, or which way it drifted. This is most difficult to decide in such widely distributed plants as *Ximenia americana*, *Ipomoea biloba*, *Remirea*, and the like. In some cases certainly the plants commenced their wanderings when the positions of land and sea areas were very different from what they are now. In the Eocene period the Nipa Palm fringed the mouth of the Thames at Sheppey, and its fruits, bored by teredos, drifted to Belgium and Italy (Rendle on "Nipadites," Linn. Journ. Bot., xxx, p. 143), just as it now fringes the Malayan tidal-river mouths. We have no trace of it on the Atlantic coast except at the mouth of the Mississippi, and it would be unlikely to have quite disappeared from the tidal rivers of West Africa and South America if it had ever reached them, and we can only suggest that there was formerly a sea-passage through what is now Eastern Africa, by which it drifted to the Malay regions.

There are, again, certain sea-borne, exclusively littoral, tropical plants common to both sides of South America, chiefly in the northern part. It is difficult to see how these can have reached both sides of the continent unless there was formerly an open sea-passage through the Isthmus of Panama.* They do not occur in temperate America, and could not have drifted round Cape Horn. A few plants are found in Burma, Siam, and then along the coasts of Cambodia, Hainan, and so to Formosa, but are absent from the Malay region. These are easily accounted for, as we know that British Malaya was cut off between the Peninsula of Siam and the modern Malay Peninsula in comparatively recent times by a strait of sea.

The main routes of importance, as far as the dispersal of plants are concerned, I am judging by the distribution of the littoral plants, the seeds or living fragments of which are transported successfully from place to place.

(1) The currents which have transported the largest number of littoral plants and spread them over the widest area are those running from the Malay regions to Polynesia via North Australia eastwards, and westwards by the Maldives, Laccadives and Mascarene Islands to East Africa, and the

* Since writing this C. Schuchert has published (Am. Ass. Report, 1928) an account of the Palaeography of the Caribbean Sea, showing that both in the Oligocene and early Pliocene there was sea connection between the Atlantic and Pacific Oceans through the Isthmus of Panama.

reverse way. By the Malay region is meant the Malay Peninsula and islands. A few of the plants in the following list may have originated in India, which I will note, and some may have gone the reverse way, i.e., from Polynesia or New Guinea westwards. (I exclude the species with a short run, e.g., *Gluta coarctata* and *Brackenridgea*), *Calophyllum inophyllum*, *Ochrocarpus* spp., *Thespesia populnea*, *Kleinhovia hospita*, *Smythea pacifica*, *Carapa* spp., *Mucuna gigantea*, *Desmodium umbellatum*, *Erythrina indica* (perhaps from India to East Africa), *Vigna lutea*, *Pongamia glabra*, *Derris uliginosa*, *Dalbergia torta*, *Strongylodon ruber* (this has apparently travelled south of the Malay Archipelago; it possibly came from Polynesia), *Caesalpinia Nuga*, *Afzelia bijuga* (possibly eastwards from Madagascar), *Terminalia catappa*, *Rhizophora mucronata* and *R. conjugata*, *Ceriops Candolleana*, *Kandelia Rheedii* (probably from India), *Lumnitzera coccinea* and *L. racemosa*, *Combretum acuminatum*, *Quisqualis indica*, *Barringtonia racemosa*, *Sonneratia* spp., *Wedelia biflora*, *Scyphiphora hydrophyllacea*, *Sarcolobus* and *Finlaysonia* (India, eastwards), *Cordia subcordata*, *Ipomoea campanulata* and *I. denticulata* (probably from India, eastwards), *Merremia nymphaeifolia*, *M. vitifolia* (probably from India, eastwards and westwards), *Operculina Turpethum* (from India probably), *Dolichandrone Rheedii* (from India, eastwards), *Acanthus ilicifolius*, *Clerodendron inerme*, *Vitex trifolia*, *Aegiceras*, *Avicennia officinalis* (eastwards and westwards), *Avicennia sphaerocarpa* (eastwards), *Hernandia peltata* (probably Indian), *Euphorbia atoto*, *Excoecaria agallocha*, *Crinum asiaticum* (probably from India), *Tacca pinnatifida* (perhaps from Africa, eastwards to Polynesia), *Pandanus fascicularis*, *Mariscus albescens* (both eastwards and westwards), *Fimbristylis spathacea*, *Scirpodendron costatum*, *Thuarea sarmentosa* (from South India, eastwards), *Cycas* (both eastwards and westwards).

Some of the above-mentioned plants have travelled north from the Philippines to the Liukiu Islands, Pescadores and Formosa, and some from India to Burma, Cambodia, Hainan, along the south Chinese coast.

To these plants must be added the tropic-wide plants *Ipomoea biloba*, *Suriana maritima*, *Colubrina asiatica*, *Hibiscus tiliaceus*, as well as some plants of Australian origin, *Dodonaea viscosa*, *Casuarina equisetifolia*, *Cassytha filiformis*, *Scaevola Koenigii* and *Spinifex*, and from Polynesia probably *Barringtonia speciosa* and *Guettarda speciosa*.

(2) Western America to Polynesia.

There are comparatively few plants which have migrated by sea to the Polynesian Islands from the western coasts of South America. *Dioclea violacea*, *Mucuna urens*, *Rhizophora Mangle*, have not travelled further than Polynesia; *Sapindus saponaria* has reached the Australo-Papuan region; *Stictocardia tiliaefolia*, *Calonyction grandiflora* have travelled through the Malayan region to East Africa; *Guettarda*, a typical American genus, probably came to the Malay region through Polynesia in the form of *G. speciosa*, though that species (the only Old World one) is not as yet known from America. It is quite conceivable that the genus *Sophora* invaded Asia from South America via Polynesia, and I have little doubt that the seashore *S. tomentosa* did so. It seems clear that *S. tetraptera*, evolved in the Antarctic regions, probably in South America, has migrated by sea as far north as Gough Island. *Apium australe* has much the same range, having travelled north from the Antarctic regions to Tristan d'Acunha and even to South Africa.

(3) Some tidal-swamp plants common to America and Africa.

There are a certain number of tidal-mud or river plants common to both sides of the Atlantic, but which Guppy's researches indicate cannot have been transmitted by sea-currents. Such are *Ecastophyllum Brownei*, *Drepanocarpus lunatus*, *Symphonia* sp., *Chrysobalanus Icaco*. *Anona palustris*, with the same distribution, may possibly have been sea-borne. *Symphonia globulifera*, the American tree, and the only species in America, is now considered specifically

distinct from the African *S. gabonensis*. But there are a number of species also in Madagascar. Now, I pointed out, in a paper on West African *Cyperaceae* of the Welwitsch Collection, that out of 129 species of Sedges, no less than 28 species were common to Africa and South America, of which 3 also were found in Madagascar, and none of these occurred in Asia, 1 species of *Cyperus* (*C. flavescens*) has gone north to Afghanistan and Europe, and 1 species of *Kyllinga* has been found (probably introduced from South America) in the Philippines. Now, these 28 Sedges are nearly all inhabitants of forests, not of open country or shore, and have certainly not been carried by man from one country to another. I point out that this is strong evidence of a former connection by land between Africa and Guiana. Studer (in " Beitrage zur Meere's Fauna von W. Afrika ") states that of 20 echinodermata 17, of 277 fish 55, of 541 gasteropods 54, occur also on the South American coasts. He attributes this to the carrying of the young or larval forms across the sea by currents, and cites the case of *Sargassum* being drifted from Florida to the Cape Verdes. It is remarkable, however, that of these marine organisms the oldest group, and one of the least likely to be so transported, the echinoderms, 85 per cent. are common to both coasts, while of fish only 20 per cent., and of gasteropods, which attach their eggs frequently to floating objects, only 10 per cent. are common to the two coasts. Wallace, who disputes the connection of the two coasts, admits that many insects are found on both shores ; but there is no connection between the mammal faunas of the country, and this suggests that the connection between the two countries was broken before the Miocene era.

If this is so, it is quite possible that *Symphonia*, *Ecastophyllum*, *Drepanocarpus* and *Chrysobalanus* formed a portion of the flora of the lost connecting land. There are a good many other species of plants as well as genera common to both continents and missing from Asia, but, as this is rather a question of distribution than of dispersal, I forbear at present to dilate on the subject.

Besides these tidal-swamp plants common to South America and Africa, we have a number of plants of which the seeds are more distinctly sea-borne. Such are *Rhizophora Mangle*, *Laguncularia*, *Conocarpa*, *Mucuna urens*, and *Dioclea reflexa*, which has apparently spread from South America and thence to Asia as far as the Philippines. *Scaevola Plumieri* appears to have migrated from South America to West Africa, then to Madagascar, and thence to India and Ceylon, where it meets with *Sc. Koenigii* coming from the Australian region westwards. *Calonyction Bona-Nox* and *C. muricata* and *Stictocardia tiliaefolia* (*Convolvulaceae*) seem to have followed the same route as *Scaevola Plumieri* and *Dioclea reflexa*, but the *Calonyctions* have been largely aided by man. *Stictocardia* seems to have migrated from South America to West Africa, thence to India by the Mascarene Islands, and then to Burma and Formosa. It is absent from the Malay region, which suggests that it passed through the formerly existing strait between Burma and the Malay Peninsula and drifted along the Cambodian and Chinese coasts to Formosa.

Sesuvium Portulacastrum probably originated in South America, as there are other species of the genus there, then crossed to West Africa, and thence along the coasts of Asia to Polynesia. *Tristellateia australasica* undoubtedly originated in Madagascar, where the remaining species occur, and migrated eastward to Malaya and Australia. *Mariscus Dregeanus* and *Lepturus repens* seem to have travelled from East Africa to the Malay regions.

(4) The Gulf Stream, conveying immense quantities of timber, fruits and seeds from the West Indies, has played a very limited part in dispersal of plants, for after leaving the tropics it passes north and, travelling past the Azores, visits the British Isles, Iceland and Norway, strewing its harvest of tropical seeds on cold shores where they cannot possibly grow.

(5) There are a few temperate climate seashore plants which have travelled

round the Arctic or north temperate region by sea, as *Ligusticum scoticum*, *Cakile*, *Honckenya*, *Mertensia*. Their area of distribution is naturally limited, by the exigencies of climate, to the cold north regions.

Summary.—I have here given an account of the routes taken by seashore plants in travelling by sea from one part of the world to another. In most cases I think that the actual route taken is approximately the correct one, but in some cases this is open to doubt, and I have only offered the conclusions tentatively. The real origin and history of the distribution of plants in this way at least will be settled, if ever, by palaeobotany and a knowledge of the earlier distribution of sea and land.

Sea-dispersal, like other dispersal methods, has not yet ceased. The recent appearance of fruits and seeds of *Barringtonia speciosa* and *Erythrina indica* on the coasts of East Africa shows this.

The sea-currents of the present day, as well as the present position of land- and sea-surfaces, are probably not the same as when the earliest phanerogams were evolved, i.e., the Cretaceous era or probably earlier. Of this at present we know little, and to lay down the routes of the travels of many plants and of their original homes of evolution would necessarily be hypothetical. We can only suggest their history, which later research will verify or disprove.

One thing remains certain, that the greater number of littoral plants are to be found in the Indo-Malayan and Polynesian regions—that is to say, in tropical regions where the areas occupied by these sea-borne plants consist mainly of islands. Along the unbroken continents, such as South America and Africa, these plants are much more scanty—at least, in number of species and genera. There is a great variation in the distances to which plants modified for sea-travel have spread, and consequently the extent of the area which they occupy. This is due in the main to the condition of perfection of the mechanism for long floating before they either become water-logged by the permeation of water through a weak point, or their tendency to early germination.

Another factor consists in the class of soil that these seeds meet with in their travels within a reasonable distance of their starting-point. Plants of the tidal rivers require to meet with a tidal river mouth, up which their seeds can be borne by a rising tide. Such spots are absent from the smaller islands, as there are no rivers of sufficient size to bring down and deposit mud at the mouth. Practically this entails an area of mountains of granite or some such material, not coral or sandstone, in the interior, which, being denuded by rain and washed down, forms the tidal mud of the river mouth and edge of the land. In fact, the geology of the interior regulates the littoral flora. In islands like Christmas Island or Cocos-Keeling Island, where the ground is built entirely or almost entirely of coral reef, neither sand-hill nor tidal-river plants can make a lodgment. Their seeds may be (and often are) thrown up on the beach, but quite fail to establish themselves. Any changes in the geology of the coastline may destroy the littoral vegetation or substitute an entirely different one. Thus tidal mud may be covered with sand washed down from sandstone mountains in the interior or thrown up by the sea. Incessant changes of this kind are in progress in most parts of the world, and always have been, and with these changes of soil there is also a change of vegetation

On a new-formed island the first flowering plants to appear are those whose seeds are sea-borne, as well as, if sufficiently near the mainland, some wind-borne plants. In Krakatau the first recorded flowering plants after the eruption were 10 sea-borne species and 5 wind-borne, but there were also 11 species of ferns. The distance, however, from the mainland is short. In Cocos-Keeling Island, of indigenous plants, early arrivals were 15 species of sea-dispersed plants and 4 or 5 plants whose seeds were adhesive to the sea-birds, bur no wind-borne plants. This is a true oceanic island, 700 miles from other lands.

Until the littoral trees have developed on a new island, no frugivorous birds come and bring seeds of baccate or drupaceous trees, nor can epiphytic plants find a lodgment. The sea-borne plants thus in almost every case form the first vegetation settlement on a new-formed island and prepare the way for other plants. This is more fully developed in "Island Floras," *see* p. 675.

Sea-transport of flowering plants and *Cycadeae* has been going on from the earliest periods of their era, and is still continuing. I have mentioned the recent migration of *Barringtonia speciosa* and *Erythrina indica* to the African coast. H. C. Robinson, visiting Cocos Island in 1911, added the following sea-borne species to the flora:—*Terminalia catappa*,* *Ipomoea denticulata*, *Fimbristylis cymosa*, *Casuarina equisetifolia*,* *Mariscus albescens*, *Eragrostis tenella*. (Those marked* may have been intentionally introduced by man.) None of these were collected by any of the several plant collectors before that date, and could not have been overlooked.

EVOLUTION OF SEA-DISPERSED PLANTS.

It will be noticed that nearly all sea-dispersed plants belong to genera which have a large number of terrestrial inland species, and that, as a rule, there are only one or two species which are adapted for sea-dispersal. Thus we have the following:—

	Species.	Sea-dispersed.
Derris	111	2
Dalbergia	237	1
Cassytha	23	1
Caesalpinia	144	3
Sophora	59	2
Spinifex	7	1
Ischaemum	80	1
Scaevola	106	2
Calophyllum	122	1
Terminalia	252	1
Crinum	153	1
Casuarina	23	1

There are a few apparent exceptions, a number of species of sea-dispersed plants which have been so modified that we keep them generically distinct, such as the *Rhizophoraceae* and *Avicennia*, and some in which the inland relations of the sea-dispersed plant seem to have disappeared, such as *Scyphiphora*, *Nipa*, *Suriana*, *Pemphis*. The *Rhizophoraceae*, which are perhaps the most elaborately adapted for a maritime and sea-transported life, seem, however, to be closely related, and are probably an evolution of the genus *Carallia*. Trimen notes (in "Flora of Ceylon," ii, 155) of *Carallia integerrima*:—"This tree very "obviously shows its relationship to the Mangroves in the large tufts of aerial "roots it sends forth from the trunk and branches." It inhabits lowland swamps near rivers, and *C. spinulosa*, of the Malay Peninsula, actually inhabits tidal swamps, though many of the other species inhabit comparatively dry inland stations, even the tops of mountains.

In the case of sea-dispersed plants of tidal mud, we must look for their ancestry on the banks of freshwater rivers. It is easy to conceive how a tree growing on a river bank can gradually be adapted to slightly brackish water, then to water containing a larger amount of salt, and so on as it pushes down the river from a position above the reach of the saline tide-rush, till it is adapted for life in pure sea-water. Simultaneously there must be a modification of seed

or fruit enabling it to be safely sea-transported to a suitable place for its development, and we have a sea-dispersed species.

In the case of the sand-shore or beach sea-dispersed plant, the original ancestor or relation is usually to be found in sandy deserts. Thus in *Spinifex*, *Dodonaea*, *Cassytha*, the larger number of allied species are to be found in the sandy deserts of Australia, and in *Mariscus dubius* those of Eastern Africa.

But in many of the other sea-dispersed beach-plants the original home of evolution is to be found where the inland forest pushes down to the seashore and meets the sandy deposits above the sea-beach, where the sand has drifted by wind from the sandy beach, or where the denudation silt from the interior of the land is pushing down towards the sea and mingling with the sand blown inwards. Here we get plants like *Elaeodendron subrotundum*, *Derris uliginosa*, *Hibiscus tiliaceus* and *Barringtonia*.

The actual history of the evolution of all the sea-dispersed flora, however, is too long a subject to be treated of here. I have contented myself with a mere sketch of the evolution as it appears to have come about. Guppy seems to think that the inland flora has largely evolved from the sea-dispersed flora. In some cases, e.g., *Dodonaea* and *Colubrina*, decidedly some of the inland species or subspecies in some countries do appear to have evolved from the littoral plants, but, as a rule, the reverse is certainly the case. The fact that a large and varied series of species of genera like *Calophyllum*, *Derris*, *Dalbergia*, etc., are found inland, and only one or two are modified for sea-dispersal, seems to settle this question definitely.

Duration of Vitality in Immersed Seeds.—Ch. Martins (*Bull. Soc. Bot. France*, iv, 324) made some experiments with seeds and fruits to test their germination after immersion in the sea for 40 days. Of those that floated, out of 20 of each seed, there survived and germinated : *Nelumbium speciosum* 3, *Cakile maritima* 13, *Cucurbita pepo* 13, *Eryngium* 10, *Asclepias cornuti* 6, *Salsola Kali* 12, *Beta vulgaris* 12, *Gingko biloba* 6, *Asphodelus cerasiferus* 2, *Pancratium maritimum* 14.

Of those that sank and yet germinated he gives *Sinapis alba* 15, *Kohlreuteria paniculata* 4, *Acacia Julibrissin* 7, *Gleditschia horrida* 3, *G. triacanthos* 4, *Rumex aquaticus* 16, *Ephedra distachya* 14, *Canna gigantea* 4.

It is doubtful whether, in the plants which he describes as floating, he intended to imply that they floated all the time, as in some cases at least (*Salsola*, *Beta*, *Eryngium*) no one else has succeeded in keeping them afloat for more than a day or two.

The importance of these experiments seems to me rather to lie in showing how long seeds floating or immersed can withstand the action of sea-water, which, if my suggestion that sunken seeds may be washed up in shallow seas with sand in storms is correct, may account for the travelling of plants from bay to bay or mud-bank to mud-bank, although the seeds or fruits do not float. The distance that such plants could travel, although not to be compared with those of floating seeds, is of some importance as allowing the plants to make their way along the coasts of a mainland. Similar experiments were made by Al. Borza and Gh. Bujoreau in Serpent Island, in the Black Sea. The seeds were immersed for a long period in Black Sea water and then germinated. All the plants experimented with were found on the island, 4 kilometres from the mainland, and the authors seem to suggest that they reached the island rather by floating on driftwood, etc., than by human agency or any other way. *Stellaria media*, the Chickweed, was one of them, the seeds of which germinated, bloomed, and fruited after 90 days' immersion.

The observers noted that the seeds actually germinated earlier the longer they remained beneath the water. In some cases, referred to under another section, the seeds germinated and the seedlings floated. The seeds experimented

with were those of *Agropyron repens* (10 per cent. germinated after 90 days), *Bromus tectorum*, *Setaria glauca*, *Festuca myurus*, *Rumex acetosa* (only a few germinated after 7 days' submersion), *Amaranthus retroflexus*, *Geranium pusillum*, *Malva neglecta*, *Anthriscus cerefolium*, *Matricaria inodora** (10 per cent. after 90 days), *Erigeron canadense*, *Lepidium ruderale**, *Portulaca oleracea**, *Bromus hordeaceus**, *Stellaria media*, *Lactuca scariola*, *Rumex patientia** *Matricaria chamomilla**. (* Seeds germinated under water and the seedlings floated.)

SEEDS CARRIED BY DRIFTWOOD AND PUMICE.

There is some evidence that seeds and fruits may be borne considerable distances on floating logs or other vegetable remains, and in the crevices of floating pumice. One may often see seeds which have fallen on leaves, branches, or pieces of board, drifting about in rivers or ponds, and the same thing occurs in sea-drift. It is a common sight to see great clumps of the rhizome of the Nipa Palm drifting along in the Malay seas, carried far away from land by currents. I have seen large masses of Bamboos, dead, lying washed up on the shores of Christmas Island, and, as mentioned elsewhere, a living clump of Sugar-cane was thrown on the shores of Cocos-Keeling Island. It is undoubtedly the fact that it must have been on such rafts as these that the endemic rats, shrews, lizards and land mollusca have arrived at the most remote islands. A considerable number of land-snails arrived in Krakatau very speedily, quite upsetting the old theory that the presence of land-snails implied a former land connection. It is not to be wondered at that on such floating arks come some seeds which had fallen on the debris before it started on its long voyage.

Guppy (in "Plants, Seeds and Currents") states that he has found seeds of *Tournefortia argentea* (*Boraginaceae*) (a seashore shrub abundant on coral islands in the Eastern Archipelago and Polynesia), in the holes of teredo in logs on Cocos-Keeling atoll, and gives a number of seashore plants as probably conveyed to different islands in the West Indies on drifting logs—*Corchorus hirsutus*, *Heliotropium curassavicum*, *Portulaca oleracea*, *Sesuvium portulacastrum*, *Suriana maritima*, *Ambrosia crithmifolia*, and *Borrichia arborescens*. All these are small plants with small seeds possessing no very ready means of transport other than on drift logs or pumice, as the seeds or nutlets do not float sufficiently long in the sea-water to travel very far. F. Wood-Jones writes (in "Corals and Atolls," an account of Cocos-Keeling Island) :—"I have seen a buttressed "tree come ashore, in an atoll, from whose base a wheel-barrow load of fine "red earth might have been collected." In such a case as this, small seeds of inland herbaceous plants might readily be conveyed to the island in the soil.

Pumice.—This volcanic product is very light and full of small holes in which seed might lodge. After the eruption of Krakatau abundance of pumice could be seen floating in the sea of the Malay region. Quantities of it were thrown up on the shores of various islands, from Christmas Island to the west coast of Singapore. Guppy writes that Mr. Ross, of Cocos-Keeling Island, says he has frequently observed seeds of *Pemphis acidula*, *Scaevola Koenigii* and *Triumfetta procumbens* sprouting from pumice on the beach. The pumice stone is usually old pumice-drift which has been washed up during gales under littoral trees, where it becomes covered with sandy soil and leaves, and seeds often drop into the crevices. When the pumice is carried off by gales and stranded on other coasts, the seeds germinate. In "Plants, Seeds and Currents," p. 291, he suggests that the following plants are transported in this way, the nutlets and seeds being previously dropped into crevices in

the pumice :—*Heliotropium curassavicum*, *Portulaca oleracea* and *Sesuvium portulacastrum*.

In the case of plants brought in this way in pumice crevices and in teredo-bored logs drifted off from distant seashores, the seeds brought would naturally be those of sea-coast plants, and might readily arrive at a similar shore to that from which they came, and successfully establish themselves there.

STEMS OR BRANCHES DISPERSED BY SEA.

It is not impossible for stems, rhizomes, or other vegetative parts of plants to be drifted away by sea and, surviving the voyage, be cast up on a distant coast. Riparian or freshwater rhizomes such as we have seen drifted down rivers, or carried by floods, are not at all likely to survive the action of sea-water, and such plants as *Pistia* and *Azolla* succumb as soon as they reach brackish water. But plants growing in tidal mud and on the seashore, and accustomed to a marine littoral life, might be transpotted to some distance.

The amount of evidence for whole plants being so transported is not large, and requires more extensive observations being made.

As I have said, great masses of the rhizomes of *Nipa fruticans*, the Nipa Palm, are frequently drifted rapidly along in the Malayan seas. Whether these masses of stem are landed safely in other tidal rivers and continue to grow there, is not certain, but I think it very probable that this does occur.

Mr. G. Clunies Ross, of Cocos-Keeling Island, told me that all the Sugar-cane which grew on the island was derived from a clump of the plant which was washed up on the shore, and which then commenced to grow. This must have come from Java, 700 miles away. Living clumps of Lalang grass (*Imperata cylindrica*) and living Bamboos have also been washed up there. It is clear that such clumps of plants might easily carry small buoyant seeds in the soil among their roots. He also states that driftwood comes in considerable quantities to this island, and at one time a crocodile, of which I saw the skull, arrived, and that on different occasions two canoes drifted there, one containing two human skeletons, the other a living native of unknown race, whose language could not be understood even by the Dutch in Java, where he was sent. He was possibly a Polynesian. This suggests a long drift from the east.

I have seen living plants of *Dendrobium crumenatum*, apparently quite green and living, floating past a ship I was travelling on, far out in the Malacca Straits. This plant occurs in Christmas Island, which, however, it might have reached by its very light seeds being borne on the wind.

Moseley writes :—" On the shores of Little Kei Island I found, on the " beach above the reach of the waves, a large mass of the pseudo-bulbs of " an Orchid (epiphytic) with its roots complete. It was partly buried at the " foot of a tree, and seemed quite lively. It had evidently been washed up " by a storm." It is rather remarkable that Orchids, which are usually so sensitive to salt water, should be able to drift safely for some way in the sea. Some species, however, are recorded as growing within the splash of the sea. In Malanopa Island, off the coast of Mindanao, Philippines, Moseley found a young Sago Palm which was just beginning to form a stem, washed up above the beach line and firmly rooted, though in an inclined position, and growing vigorously (" Notes of a Naturalist," p. 368).

I believe that *Sesuvium portulacastrum* is transported from one place to another by its branches being drifted about, and perhaps the succulent *Philoxerus vermicularis* can be so dispersed. Sernander states that portions of *Honckenya peploides* are distributed by sea.

The rhizomes of some of the seashore grasses, such as *Paspalum vaginatum* and *Spartina stricta*, and *Elymus arenarius* and *Psamma arenaria*, are sea-dispersed.

The rhizomes and creeping stems of marine flowering plants, such as *Zostera*, *Halophila*, and *Enhalus*, are often torn up by storms, and may be transported to distant spots where they may establish themselves.

Spartina Townsendi.—This sea-mud plant is now common on parts of the English coasts and South Europe, and has been planted in New Zealand, and occurs also in South Africa. H. S. Thompson says it has a fairly long rhizome, and he records several clumps occurring on the Berrow Flats near Burnham-on-Sea, Somerset, probably carried by the tide from south of Clevedon (a distance of 14 miles north-east), where it had been planted. F. W. Oliver (*Gardeners' Chronicle*, March 20th, 1926, p. 212) describes a marsh swamp at Havre which M. Duteutre says formerly carried mainly *Salicornia herbacea;* then came *Aster tripolium*, then *Spartina Townsendi*, then *Glyceria maritima*, each plant in turn driving out the other. Dr. Stapf found specimens of rhizomes cast on the shingle-beach between Milford and Hurst Castle, two of which were still alive. Several other species occur in other parts of the world, growing in fresh water, or in saline marshes in America, one of which ranges to Brazil, and down as far south as Patagonia.

S. arundinacea forms tussocks in Amsterdam Isle, Tristan d'Acunha, Gough Island, St. Paul's Isle, Inaccessible and Nightingale Islands. It has probably been carried by sea to these spots, but whether by rhizome, or clump, or by seed, is rather doubtful. It is clear, however, that the *Spartinas* generally are dispersed by portions of rhizome drifting in the sea.

It is probable that some other of the tidal-mud species of grasses are also drifted by fragments of rhizome to distant coasts. Such are the following :—

Myriostachya Wightiana.—This has a thick spongy root-stock covered with roots. It is found in Ceylon, Sunderbuns, Tenasserim, Siam and Penang, Aden, east coast of Africa, Somaliland, Ranga Isle and Guzerat, Scinde, Cape Comorin, Tuticorin. It appears to be a habitant of sandy beaches rather than mud. It has a rhizome, but may have travelled down the coasts of both sides of the Indian Ocean by seed.

Sporobolus virginicus, a sand-shore plant with a woody root-stock. It must be sea-dispersed. It is found in the Mediterranean, tropical Africa, Ceylon, Australia, New Caledonia, Marianne Islands, Hawaii, West Indies and South America, Galapagos and South Trinidad. It seems mostly absent from tropical Asia, and may be of American origin and brought to Colombo, etc., in ballast. Trimen says it rarely flowers in Ceylon, and the flowers are imperfect and sterile. It is very unlikely that the small seeds of this plant should have reached South Trinidad and Galapagos by sea-floating, and it has probably migrated by the basal stem drifting in the sea.

Glyceria (*Sclerochloa*) *maritima* is European, occurring also in Iceland and the Faroe Islands and Arctic America. It is tufted with prostrate barren branches, and is probably drifted by sea in this way. It is found in the tidal mud.

Elymus arenarius, of sand-hills in Europe, Iceland, Labrador, Arctic America, San Juan Isles, Washington, Disco Isle, Greenland, Kamschatka, and an allied plant at Port Famine, South America, having a long rhizome; and *Psamma arenaria*, a sand-hill plant, also rhizomatous, spread from Europe to Palestine, North America to Newfoundland, Virginia and Quebec, are probably both spread by drifting rhizomes.

I add here the following note by H. A. Gleason and M. T. Cook (in the "Plant Ecology of Porto Rico," New York Academy of Science, vii) :— "Occasional small mats exist (on the seashore) of *Opuntia Dillenii* and *O. repens*. "They are derived from joints washed down by waves from the thickets

"above and left stranded on the upper beach." They agree that these mats are usually sooner or later washed away by the sea, and do not establish themselves, but alterations in sea-level or sufficient deposit of silt to push the sea back might allow of their establishing themselves.

MARINE SUBMERGED FLOWERING PLANTS.

There are a number of marine flowering plants belonging to the orders *Hydrocharidaceae* and *Naiadaceae*, rhizomatous plants growing in shallow water, usually in sand or mud, along the coasts. In most of these the fruits are soft, and neither they nor the seeds float, though they may be drifted along the coasts on the sand by currents to some distance. In most of the tropical regions in which we find these plants they form the food of *Halicore* and *Manatus*, the Dugongs and Manatees (*Sirenia*), and turtles (*Chelone mydas*) also feed on them and might swallow the seeds, although, as these are usually very soft, it is unlikely that they would pass through their bodies unharmed. It is much more probable that their dispersal is effected simply by the drifting of portions of the rhizome broken off by the waves, in much the same way as the marine *Algae* are dispersed. *Zostera* is said to be largely the food of Brent geese, and it is suggested that portions may become attached to these birds while feeding and be so transported.

Enhalus acoroides (*Hydrocharidaceae*) has a stout rhizome, and grows in quiet muddy bays, usually in great abundance, with long linear grassy leaves. The fruit is 1½ inch long and 1 inch through, containing a small number of soft seeds. It is borne on a long peduncle, which during the flowering period is erect, so that the female flower is at the surface of the water, and is fertilised by small floating male flowers detached from the inflorescence, after which the peduncle contracts in a spiral manner so that the fruit ripens under water. Detached portions of the rhizome are commonly to be seen floating at the surface of the sea, and cast up on the shores. It has a long range of distribution, being found in the Red Sea and on the coasts of Madagascar, Ceylon, the Malay Peninsula and islands, to the Philippines and Liukiu Islands, Australia and New Caledonia.

Thalassia testitudinarum, a native of West Indian seas, and *Th. Hemprichii*, which occurs in the Red Sea, East Africa, Seychelles, Ceylon, Borneo, New Caledonia and the Liukiu Islands, resemble *Enhalus* in general appearance and habit, but the fruits have many small seeds. They are largely eaten by turtles, which might eat the fruit and pass the seeds, but they are also dispersed by the breaking up and drifting of the rhizomes. Trimen (in the "Flora of Ceylon," iv, 128) says that during the south-west monsoon the latter is washed ashore in large quantities at Jaffna.

Halophila, a genus of which about 7 species, mostly very similar, have been described, has slender filiform rhizomes and thin, long-petioled small leaves. The fruits are small beaked utricles with about 12 minute globose tubercled seeds. They range in shallow seas to a depth of 18 feet, from the Red Sea to Madagascar, Madras, Ceylon, the Malay Peninsula, Borneo, Aru, Australia, Tongatabu and to Tonkin, Liukiu Islands and China, with 3 species in the seas of the West Indies and Florida. In both hemispheres they are found washed up with various *Algae* after a storm, and bits are often to be seen drifting in the sea.

Posidonia.—This genus, like the following genera, belongs to the order *Naiadaceae*. *P. caulinii* is a plant of the habit of *Enhalus*, with a stout rhizome and grass-like leaves, a native of the Mediterranean Sea. The fruits are 1 inch long and 1-seeded. They do not dehisce, but germinate in the pericarp. Masters (note in Kew Herbarium) says that he has found them thrown along the

shores of the Mediterranean Sea, and apparently they are rather light, but bits of the rhizome are also torn up by storms, and no doubt the plant is thus mainly dispersed. Of *P. australis*, a native of the Australian seas, von Mueller notes that fish eat the seeds as soon as they are forming (note in Kew Herbarium). *Amphibolis*, an Australian plant, has much the same habit, but has a more slender rhizome.

Zostera is a genus of 2 or 3 species, of which the most widely spread is *Z. marina*, an inhabitant of shallow water in Europe from the Mediterranean Sea to the Arctic regions, Kamschatka, Japan and North America. It has much the habit of *Posidonia*, and the rhizomes are often seen drifted up on our shores after a storm. *Z. nana*, a smaller species with a more slender rhizome, is more of a warm-water plant. It occurs in Europe as far north as North Denmark, Germany, in the Mediterranean, Canaries, South Africa, Madagascar and Tonkin.

Pectinella (*Cymodocea*) *antarctica* is a very remarkable marine plant described and figured by J. M. Black (Trans. Roy. An. Soc. S. Australia, xxxviii, pl. I). The plant is a native of the Australian seas, with the habit of a *Cymodocea*, an erect stem with ribbon-shaped leaves in two rows. It is dispersed, like all this class of plants, by fragments of the rhizome being detached and drifted about; also, according to Kerner, by off-shoots. The lower leaves fall off the stem, and the upper part becomes much modified, the internodes much contracted. At the lowest node a 4-lobed scale leaf is developed, which surrounds the leaves of the upper node like a cup. Buds arise in the axils. The scale leaf decays, leaving the stiff veins in the form of a comb, and the shoot breaks off below it and is drifted away. It is eventually anchored by the comb and commences to grow.

Mr. Black describes the reproduction by seed thus :—" The female flower ' consists of twin carpels on a peduncle, one of which is often abortive. A ' row of membranous bracteoles encloses the flower, being united in the ' form of a cup. Four small truncate lobes appear from the middle of the ' carpel after fertilisation, and grow and spread outwards, resembling a perianth. ' These develop a horny framework inside, and are fleshy outside, the tubular ' part of which forms the innermost layer of the pericarp, and protects the ' growing embryo. When ripe the base of the style splits, and the plumule ' emerges into the water. The top of the pericarp decays, and there remains ' the 4-lobed comb, now cut into from 10 to 20 subulate teeth. The comb breaks off from the end of the branch and sinks. Its teeth catch in the fibres ' of *Posidonia australis*, or other material on the ground, and so the little plant ' is anchored, and cannot drift into water too deep."

The distribution of these plants is very instructive. In the first place it will be noticed that the Mediterranean species are absent from the Red Sea, and those of the Red Sea are wanting in Europe, though the land separating these two bodies of water is very narrow. There is no sign of their having ever been distributed by birds. Now that the Suez Canal connects the two seas, it is not improbable that the European species may enter the Red Sea, or that those of the Red Sea may pass into the Mediterranean. Only one of these plants is common to the Old and the New Worlds, *Zostera marina*, which, being an inhabitant of cold regions, can be traced to America from Northern Europe, via Kamschatka or by the European and American Arctic islands.

None of the tropical species have crossed the Atlantic, and all are scarce round distant islands. The greatest number of species are found in the Red Sea and along the African coast, and seem to have drifted south and east to India, Ceylon, and along the Malay Peninsula and Archipelago to Australia and Fiji, and northwards to China.

The marine *Naiadaceae* seem to be quite absent from the Straits of Malacca and most of the Malay Islands except those nearest to Australia, and are absent also from Peninsular India, except the extreme south, but reappear in Australia, suggesting that they have drifted along the west and south coasts of Sumatra.

ALGAE.

The spores of the marine *Algae* are, it seems, very short-lived, and by the drifting of these the *Algae* are comparatively little dispersed, at least to long distances. They seem rather to be dispersed by fragments, or whole plants borne on the currents. Sargasso weeds (*Sargassum*) float free always, and of course can travel wherever currents take them, being probably only limited by the temperature of the water. Fragments (dead) have been found on the coasts of the Azores, Cornwall and the Shetlands. *Sargassum* is very abundant in the Red Sea, and I think I have seen it in the Suez Canal, so that it may eventually reach the Mediterranean. According to Hedley (*Journ. Proc. N.S. Wales*, i, 1915):—" In Sydney Harbour occasionally the Zosteretum " (area covered by *Zostera*) is invaded by *Colpomenia sinuata*, the Bubbleweed. " When the gas forms in the expanding balloon, it lifts the shell to which it " is attached, oyster, whelk or cockle, and floats it away." F. W. Flatteby (in " Biology of the Seashore ") says :—" Currents disseminate seeds and spores " and break off and transport shoots of *Zostera*, *Ulva*, *Fucus*, etc."

Sauvageau (" Sur le dissémination et la naturalization des algues marines," Bull. Inst. Oceanograph. Monaco, 1918, 42, p. 28) writes :—" The motility " of reproductive cells is an inconsiderable factor in dispersion in comparison " with currents. The red *Algae* are not at any material disadvantage on account " of their non-motile sperms and spores. The extension of range is largely " by reproducing fragments carried by currents, also shore *Algae* by attach- " ment to floating logs, ships, etc. The pieces of *Algae* transported thus to " unsuitable localities for reproduction may maintain their growth for years."

TERRESTRIAL FLOWERING PLANTS WITH SEEDS DISPERSED BY SEA-CURRENTS.

I here propose to give an account of the Phanerogamous and Gymnosperm plants which owe their distribution to the dissemination of their seeds to transportation by sea-currents—that is to say, they can be successfully carried from one coast to another, and from one island to another, and establish themselves on distant lands by the aid of their buoyant fruits or seeds. Plants of which only dead fruits or seeds are commonly cast up on remote shores are here excluded. They have been dealt with under the heading of River-Dispersal on pp. 197-241. The species are arranged in scientific order for convenience.

ANONACEAE.

Anona palustris.—The genus *Anona*, with the exception of this West African plant, is exclusively American. The fruits are nearly unique in the order, inasmuch as the usually separate carpels are connate into a globose or ovate heart-shaped head. In most of the species the whole mass is juicy and sweet, but in *A. palustris*, which grows in the tidal mud, it is hard and almost woody. In the other *Anonas* the seed is dispersed by birds or mammals. Harshberger suggests that the dry fruit of *A. palustris*, too, is locally bird-

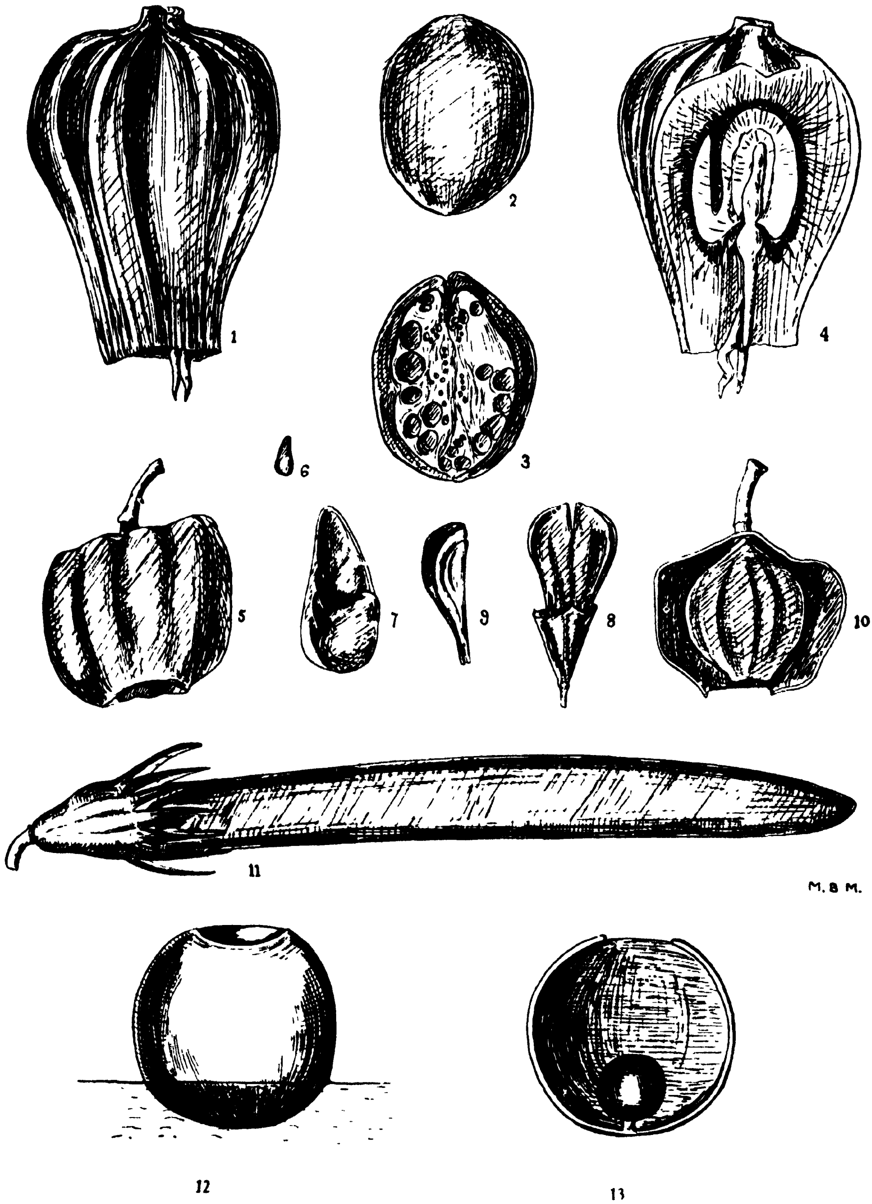
dispersed, and it is also stated that it is eaten by alligators (whence its name Alligator Apple), iguanas, and such animals. There is, however, very little doubt that it is sea-dispersed. It occurs in tidal estuaries and Mangrove swamps in the whole of South America, from Florida southwards, on both Pacific and Atlantic coasts, including the Galapagos Islands, and on the west coast of Africa in the Senegambia and Niger region.

The seeds are oblong, flattened, smooth and hard, with a layer of buoyant tissue beneath the hard outer testa. They are set free from the fruit by its decaying after it has fallen into the sea. Guppy found them floating in abundance in the drift of the river at Guayaquil, and many in a germinating condition. He saw them also floating in the Gulf of Guayaquil 10 to 20 miles from the mouth of the estuary, and thrown up on the beaches 30 miles to the south. He found that they would float for 11 weeks, none sinking, though several had become putrid. The tendency to germinate when floating in rivers is, as he says, much against their dispersal by sea to great distances, since sea-water would kill the germinating seed. Still, as bushes grow among the Mangroves practically in sea-water, the seeds must certainly be able to germinate and develop in very saline mud. The bushes also grow in the inland regions of South Florida around freshwater lakes (Harshberger). This may be due to the shifting of the coastline, so that what was formerly brackish or salt water is now fresh, and the *Anona* has persisted, as other littoral plants have done inland elsewhere, or the plant may have been originally an inhabitant of freshwater swamps which has later taken to a littoral life. The interesting point about this plant is its occurrence on both sides of the Atlantic Ocean. In this it resembles the tidal marsh plants *Symphonia*, *Drepanocarpus* and *Chrysobalanus* (later described); but though the fruits and seeds of these plants have little or no adaptation for sea-transport, *Anona* seed can float for a very appreciable period in a germinable state. Guppy, basing his remarks on the duration of the floating period of the seeds, shows that they might have been transported by sea from Africa to America by the equatorial current, a passage of two or three months only; but as the *Anonas* and their allies, with the exception of this species, are all American, it is not at all likely that it can have invaded America from Africa. The passage from America to Africa by the counter-equatorial current would take from 6 to 8 months, too long for the seeds to last in a sound condition.

We cannot be sure that the currents have always been the same as they are now, or that there have not been connecting land or islands between the two countries. I have gone into this question elsewhere. There can be no doubt that the seeds can be dispersed by sea, and they have been spread in this way along the coasts of America; but assuming the land of America to have always been as it is now, it is difficult to see how this seashore plant, as well as some others exclusively littoral, can have spread to both coasts. It certainly could not have been drifted by sea southwards to Cape Horn and up the coast to Ecuador (but see note p. 246). It is abundant apparently on the tropical west coast, and has reached Galapagos. From the mainland on the west it could have been sea-drifted to these islands, but as the fruit is believed to be eaten by the big lizards, it might have been conveyed to them by the large vegetarian lizards which haunt the Galapagos. I did not find it in Fernando de Noronha, but suitable localities for it were restricted there. It was abundant on tidal rivers in Pernambuco, 200 miles away. The distribution of this plant suggests a very considerable change in land surfaces since its first evolution.

No other species of the order is known to be sea-dispersed, and the *Anonaceae* are absent from all oceanic islands except the Galapagos, as mentioned. Hemsley records the occurrence of carpels and seeds resembling those of *Polyalthia* and *Artabotrys* in the New Guinea drift, but apparently

PLATE XIII.



SEA-DISPERSAL. FRUITS AND SEEDS.

FIG. 1.—*Nipa fruticans* (fruit, reduced).
,, 2.—*Saccoglottis amazonica* (fruit).
,, 3.— ,, ,, (in section).
,, 4.—*Nipa fruticans* (fruit, in section).
,, 5.—*Hernandia peltata* (fruit in enlarged calyx).
,, 6.—*Morinda citrifolia* (seed, enlarged, after Schimper).
,, 7.— ,, ,, (,, in section).
,, 8.—*Clerodendron inerme* (fruit, enlarged).
,, 9.— ,, ,, (one carpel).
,, 10.—*Hernandia peltata* (fruit calyx, in section).
,, 11.—*Bruguiera gymnorhiza* (fruit germinating).
,, 12.—*Hernandia ovigera*.
,, 13.— ,, ,, (calyx, in section).

not in a condition for germinating. Nearly all the plants of this order are dispersed by birds or mammals. Guppy found seeds of an Anonaceous plant in the sea-drift of Cocos-Keeling Island, but these might have been from a fruit of one of the cultivated *Anonas* on the island.

CRUCIFERAE.

Cakile maritima and allies.—All the species of this seashore genus are very closely allied. The conic fruit with a 2-horned base, which floats, consists of the upper joint, which contains a spongy light tissue by which the seed, which is too heavy to float, is supported. This indehiscent joint breaks readily off and drifts away. Martins records that in *C. maritima* the fruits germinated after being 45 days in the water, but (Guppy shows) they do not *float* for more than 10 days. Consequently we may argue that fruits which have sunk anywhere near the shores in shallow water may safely be thrown up in sand after a storm. The cause of their sinking is due to the water penetrating the suture of the lateral halves of the pod at its base. The variation of this slit in size causes the variation of the floating period of the fruit, as does the variation of the amount of the spongy tissue in the fruit. *C. alacranensis*, from the Alacran shoals, North America, which has fruits with unusually large spongy tissue, floats for 20 days ; fruits of *C. lanceolata*, in Jamaica, from 25 to 35 days ; those of *C. maritima* from 7 to 10 days.

Guppy points out a difficulty here. *C. lanceolata* occurs on the Cayman Isles, Alacran shoals and Bermudas, and it is the species showing the greatest buoyancy. The drifting of the fruits from the West Indies to Bermuda would occupy from 10 to 12 weeks. Similarly, for the occurrence of *C. maritima* in Iceland, the fruits of which float but from 7 to 10 days, while the Faroe Islands, the nearest land, is 250 miles away, it would be easier, he says, for the fruits of the West Indian species to reach Iceland in the Gulf Stream drift than for *C. maritima* to cross from Europe. The passage from the West Indies would occupy many months, and the climate of Iceland would not suit the West Indian plant.

There are two possible factors which I think should be taken into account —one is the action of drift ice, which might convey these fruits for a long period if they were frozen into it, and the other is their being entangled in floating seaweed. I have observed floating seeds and fruits of different plants in some abundance entangled in confervoid *algae* in fresh water, and remaining floating thus for some months. Guppy, however, looks for the explanation of this dispersion of the genus in Arctic latitudes as occurring at a time when warmer climatic conditions prevailed.

C. maritima occurs on most of the coasts of Europe, in Iceland, the Faroe Islands, Algiers and Palestine, *C. edentula* in the Azores and Canaries, *C. americana* in North America and on Cozumel Island, Yucatan, *C. lanceolata* in Jamaica and the West Indies generally.

C. maritima was in Australia before 1867. It was no doubt transported there in sand-ballast.

Crambe maritima, the Sea-Kale, has floating fruits somewhat after the style of those of *Cakile*. The fruit is globose, ¼ inch through ; the pericarp is thick and of a loose spongy texture. The seed does not completely fill the space in the pericarp, and there is also a space between the cotyledons. The seed is, however, non-buoyant, but the husk readily floats. The fruits float, according to Sernander, for 13 days ; Martins says 45 days ; and Darwin found they germinated after immersion in sea-water for 37 days, but does not say they floated all the time. The plant seems confined to the beaches of Europe. I have usually seen it growing sporadically in shingle. It is by no

means so abundant or widespread as is *Cakile*, although its fruits have actually better floating powers. The remaining species of the genus are inland plants with smaller pods, not at all adapted for dispersal by water.

CARYOPHYLLACEAE.

Honckenya (*Arenaria*) *peploides*.—This little succulent herb with its fleshy few-seeded capsules is an arctic plant, which goes as far south as the coasts of Portugal and as far north as the north of Norway, Faroe Islands, Iceland, Arctic Siberia to Kamschatka and Behring Straits, Kolguev, Japan, Jan Mayen, Labrador and Fidalgo Island, Oregon. The seeds float for over a year, and their buoyancy is rather remarkable. The testa is thin, and the embryo, which is non-buoyant, is curled round a loose spongy albumen by which the seeds float (Guppy). He states that 75 per cent. float for over a year, and never germinate in salt water, but when transferred to fresh water germinate healthily in a few days. They only float a few days in fresh water, all sinking in 10 days. Very few seeds are known to float in sea-water and sink in fresh, as nearly all other seeds which float in salt water float equally long in fresh. Sernander says the capsules float also, but as they dehisce, this is of comparatively little importance. He says that floating portions of the plant are also dispersed by sea.

PORTULACACEAE.

Portulaca oleracea has been frequently classed as a sea-dispersed plant. I have given an account of it under Plants Dispersed by Human Agency, p. 653. It certainly does occur sometimes on sea-beaches, but it is remarkable that it has not reached Krakatau (1919), though it is common in Java ; nor did it arrive at Christmas Island till after many weeds had appeared, and then only grew with them. Hemsley records it from Bird Island, Seychelles, as 1 of 6 plants found there, the other 5 being sea-borne, and on Malden, Caroline Islands, and Diego Garcia, to all of which it was apparently sea-borne. But its wide distribution is mainly due to man. It was common in Fernando de Noronha, chiefly in cultivated ground, but I also found it on Rat Island, an island of the group, almost, if not completely, devoid of weeds of cultivation, and uninhabited. It may possibly be transported on drift logs and in pumice (*see* p. 252) occasionally.

GUTTIFERAE.

Calophyllum is a large genus of trees or shrubs, very abundant in tropical Asia, and scantily represented in Polynesia and South America. The fruits are globose or oblong, green (rarely yellow) drupes, with a thin epicarp. They are dispersed by rolling when fallen, and often by birds and bats. *C. macrocarpa*, a riverside tree, has large fruits apparently river-dispersed. One species, however, is very widely sea-dispersed, and has far the largest distribution of any plant of the order.

C. inophyllum, a big spreading tree, with globose fruits 1 inch through which float easily for a long time, is found on most coasts from East Africa to Polynesia. Moseley describes it as the most abundant littoral tree which forms the first vegetation on coral islets, and, indeed, it is only absent from islands and coasts in some way unsuited to its growth between Zanzibar and Samoa. It grows almost equally well on sandy coasts and coral beaches and reefs, though in Christmas Island it was confined to the basaltic outcrops. Frequently planted inland for ornament, it seldom thrives or attains its full size, and even where it becomes large and fruits abundantly, it hardly reproduces itself. It is, in fact, a typical seashore plant. It occurs scantily in Zanzibar, in Madagascar, Seychelles, Comoro Isles, Mauritius, Aldabra, Bombay, Madras,

Ceylon, Andamans, Nicobars, Malay Peninsula and islands, including Cocos-Keeling, Sipora Isle (Sumatra), Little Kei, Christmas Isle, Hainan, Formosa, Liukiu, Bonin, Timor Laut, Albany Isle (North Australia), Cook Isle, Fiji, Samoa, and most of the Polynesian Islands, but is absent from West Africa and South America. It occurs in Hawaii, but, according to Hillebrand, as an introduced plant only. However, Guppy found a fruit in the Hawaiian beach-drift, so it is possible that it may be indigenous. It is interesting to note that, as in some other coast plants, the native name Vintan (Polynesia and Madagascar) and its modification, Bintan or Bintangor, ranges over the whole area, exclusive of the India region. This does not imply that the plant has been introduced by man to all these regions, but merely that the travelling Malay and Indonesian people recognised it in the various localities they voyaged to.

The floating power of the fruits is due to the light kernels of the seed, aided by a layer of air-bearing tissue between the shell and the seed. The shell is thin and rather brittle. Schimper found they floated for 126 days.

Calophyllum Calaba is a Central American and West Indian species. The fruits of this resemble those of *C. inophyllum*, and have the same buoyant tissue. It is not a littoral tree, but occurs inland in Jamaica and Cuba. Guppy found some sound seeds on the Jamaica beach and on Turk's Island drift, but notes that the fruits floated sound for 2 or 3 weeks only, and thinks that the fruit shell is more pervious to water in prolonged flotation. It seems to have made no progress in sea-travel, for probably it fails to grow on sandy or gravelly sea-beaches, and has failed to reach the shores of Florida and the Bermudas. A specimen from Hawaii in Kew Herbarium is perhaps from an introduced tree.

Schimper found that an inland species of *Calophyllum* (*C. amoenum*) had buoyant fruits, and Guppy found that *C. minus*, an inland tree of the Solomon Islands, also had floating fruits, and showed that the diminished buoyancy of the inland fruits is due to the diminution in thickness of the buoyant shell, which is thickest in the seashore species.

Ochrocarpus.—A small genus of trees allied to *Calophyllum*, some inland and some seashore trees. The fruits are oblong or sub-cylindric, 1-seeded, with a rather corky, woody epicarp. There are three Asiatic ones on sea-coasts or a short way inland—*O. longifolius*, Bombay to Madras; *O. siamensis*, Siam, north of the Malay Peninsula, by the sea; *O. ovalifolius*, sea-dispersed; and several African and Madagascar species. None of these are as widely sea-dispersed as *O. ovalifolius*, which is a typically insular plant, found on Pulau Sangian, Christmas Island, Solomon Islands, Timor Laut, Fiji, and Observatory Isle in the Admiralty Islands. The fruit is conic oblong, about 1½ inch long. It is curiously absent from the larger islands or mainland. In Christmas Island I found a number of fruits which had been carried under a rock and gnawed to bits by rats. It is possible that the comparative scarcity of the plant is due to the destruction of the fruits by these rodents.

Garcinia mangostana, the Mangosteen.—I have seen fruits of this tree cast up on the shores of Cocos-Keeling Island, where it is not cultivated, and once I picked up one on the Chesil Beach, Portland. It has also been recorded as drifted up on one of the Lofoten Islands, Norway, by Lindman in 1879. These were no doubt all fruits thrown overboard from ships coming from the Malay region. The tree is only known in cultivation, and the soft seeds have a very short period of vitality, and would be at once destroyed by sea-water.

MALVACEAE.

Hibiscus tiliaceus, a rather large tree with capsular fruit, ovoid conic, containing a number of small seeds. It is abundant on sea-coasts, usually in gravelly or clayey places, also on coral rocks, and is one of the most widely spread

of sea-dispersed plants, occasionally found inland, but almost always planted there as a hedge plant, or grown for ornament. It occurs on sea-coasts in India, Bombay, Sundribuns, Ceylon, Pegu River, Little Coco, Malay Peninsula and islands, including Timor, Christmas Island, Krakatau, Cocos-Keeling, Papua, Philippines, North Australia, all Polynesia, Mexico, West Indies, Brazil, New Granada, Galapagos, West and East Africa, Madagascar, Mascarene Islands. Lefroy records the germination of seeds washed ashore on the Bermudas. It is absent from Aldabra, Socotra, and some other islands, probably climatic condition being unsuitable for it. The capsules open on the tree and release the seeds. According to Guppy, the floating power is derived from the spaces between the folded and crumpled cotyledons and the testa, but neither the seeds nor fruit have any buoyance of themselves. They float for months, and are common in sea-drift. Guppy and Schimper kept 6 sound seeds floating for 40 days, but none germinated.

Thespesia populnea, a tree much resembling *Hibiscus tiliaceus*. The capsule is round and hardly dehiscent. It is very widely spread on sea-coasts in Asia and Polynesia, but less widely dispersed than *Hibiscus tiliaceus*. It is found in the Liukiu Islands and Hongkong, Hainan, Ceylon, India (apparently only planted), Andamans, Mergui, Siam, Malay Peninsula and islands, including Aru, Timor Laut, Cocos-Keeling, Admiralty, Australia, most of the Polynesian Islands, Guiana, West Indies and West Africa (dubiously native), East Africa, Europa Isle, Mascarene Isles, including Aldabra.

It is often used as a roadside tree, and appears in the Cape Verde Isles as such, and probably this is its origin in South America and West Africa. The fruits, after a week in the sea, break up and the seeds escape. The seeds float by the aid of the air-spaces between the folds of the cotyledons, as in the *Hibiscus*, and Guppy germinated seeds successfully after a year's flotation in sea-water, in spite of their being exposed to a temperature low enough to freeze fresh water.

STERCULIACEAE.

Heritiera is a small genus of *Sterculiaceae* allied to the forest trees *Tarrietia* found in the Indo-Malayan region. One or two species of *Heritiera* are large tall trees which grow in the forest far away from river and sea, but the majority of the trees are not so lofty, and grow in tidal swamps or on river banks. The line of evolution of these plants from *Sterculia* is suggested under Wind-Dispersal (*see* p. 84).

H. fomes is found in the Sundribuns of Calcutta, the banks of the Ganges, and in Burma. The fruits are rounded, cone-shaped, about 1½ inch long, and contain a large starchy seed with an air-space between the cotyledons, which is the cause of its buoyancy. Troup (in "Sylviculture," I) writes of it as follows:—

"In the spring tides of August the masses of seeds on the surface of the "water have the appearance of immense rafts, so closely do they float to- "gether. The forces operating on its dissemination are the strong floods of "river water and local rains seawards, the spring-tides, which occur at this "season, and the monsoon winds blowing from the south-west. The last "factor is evidently the important one, as seedlings are often found in quantity "on the north and east banks of the larger rivers, where they have been washed "by the waves formed by the monsoon winds."

This species, though possessed of very buoyant seeds, has migrated to a distance comparatively short, when contrasted with the extremely wide area invaded by *H. littoralis*, of which the fruits are even better adapted for sea-dispersal. In this tree the fruits are much larger, from 1½ to 2½ inches

long, elliptic-oblong in shape, with a strong keel and a thick, fibrous corky pericarp. The tree grows only in tidal swamps mixed with Mangroves, and ranges from Zanzibar and the Mascarene Islands to India on both coasts, Little Coco, the Malay Peninsula and Archipelago, including Krakatau, to Australia and Polynesia, as far as Fiji. It is absent from Cocos-Keeling (though I had specimens of fruits washed up there) and Christmas Island, and other islands and stretches of coast in this area where there is no tidal mud for it. It has failed to reach Hawaii.

The seed, which is said by Guppy and Schimper to be non-buoyant, does not completely fill the cavity of the carpel, but leaves a space which causes it to float. The light fibrous coat of the carpel, however, is probably the most important factor in its buoyancy (Pl. V, figs. 4 and 5).

Kleinhovia hospita.—This beautiful tree owes some of its distribution in the African region, Siam, India and Ceylon, to introduction by man. It is certainly wild in the Malay Peninsula, Borneo and Java, and the Eastern Malay Islands, including Christmas Isle, the Philippines and New Guinea, Timor Laut, Australia, Samoa, Fiji, Tonga, Solomons, Hainan and Formosa (seashores). It certainly grows in many places inland, often on river banks, but is also a seashore plant in New Guinea, Christmas Island, and some of the Polynesian Islands. Guppy (who records it as a plant of East Africa, Mascarene Islands and India, where it is undoubtedly an introduction) says that in the Solomon Islands the natives affirmed that it was distributed by parrots, which ate the fruits. The capsule dehisces on the tree; it is swollen and bladdery. He found that in the seeds of the littoral form in Fiji, 30 per cent. of the seed floated after 10 weeks; but Schimper found that seeds (probably from Java) sank at once, and he seems inclined to attribute its dispersal to birds. I think it is sometimes sea-dispersed, but when inland, by river, and to some extent by wind blowing the light fruits about.

Melochia arborea (*M. velutina*).—This tall shrub is a native of tropical Asia, and is commonly found inland. The fruits, in large corymbs, are capsular, and contain a number of small flat-winged seeds, the wing being terminal, oblong, rounded at the top, $\frac{1}{4}$ inch long. Inland this plant is naturally readily dispersed by wind, but there can be no doubt that it is also sea-dispersed. It is found in India, but usually cultivated only, also in Mauritius and Madagascar, possibly also introduced here. It is certainly wild in Burma and the Malay Peninsula, Siam and Cambodia, and is also found in the Nicobars, and in all the Malay Islands from Sumatra to Papua, even in Timor Laut, Little Kei, Ternate, etc., also in Christmas Island and Krakatau (1897). Allied species occur in Polynesia. Now, it is clear that this plant cannot have arrived at the two last-mentioned islands by its seeds having been blown across the sea, and it cannot be doubted that they arrived by floating The seeds, which much resemble the fruits of *Casuarina*, are distributed, as those are, both by wind and water.

TILIACEAE.

Triumfetta.—There are 2 or more species of this genus, which are prostrate creeping plants in sea-sand. The fruits are globose and spiny, from $\frac{1}{4}$ to $\frac{1}{2}$ inch through. Of both *T. procumbens* and *T. subpalmata* Guppy says the fruits float.

T. subpalmata is found in sandy seashores from Cochin China and the Malay Peninsula to Java, Borneo, Cocos-Keeling to the Philippines and islands off Australia.

Ross says that he has found them adhering to booby's feathers in Cocos, but as sea-birds are local or absent in the other localities mentioned, the fruits are doubtless mainly sea-dispersed.

MALPIGHIACEAE.

Tristellateia australasica.—Except for this one, all the other species of the genus are inhabitants of Africa and Madagascar. They are climbers, with panicles of yellow flowers and winged fruit of 3 carpels, each carpel having from 3 to 8 wings. In *T. australasica* the wings are reduced, and corky or woody. The 3 carpels separate, fall off into the water, and are drifted away. The plant climbs over bushes and trees in the Mangrove swamps, but it is readily grown in tropical gardens, and is very popular from its masses of bright yellow flowers. It is found in Siam, the Malay Peninsula, Formosa, Malay Islands to the Philippines and New Guinea, Aru, Talauer, Timor Laut, Australia, New Caledonia, and Solomon Islands. It is one of the few plants in which the winged fruit or seed has been modified for sea-dispersal by their becoming more rigid, corky, and woody, and it is by these very light woody wings that the seed is floated. It is interesting to note that there is a large area between Madagascar and the Malay Peninsula where no species of the genus occurs, although the plant must have been derived from one of the Madagascar species. None of these are at all modified for sea-dispersal, though some grow on the seashores. The most nearly allied species to *T. australasica* appears to be *T. Bojeriana*, in which the wings are stiffer and shorter than in most species.

SIMARUBACEAE.

Soulamea amara, a small coast tree. The fruit is flat, heart-shaped, ½ inch long and as wide in the widest part, with 2 small seeds. It is a coast tree in Polynesia, Papua, Gebeh Island and Borneo. There are several species in New Caledonia, mostly with flat-winged fruits, and *S. terminalioides*, of the Seychelles, has 3-winged fruits. There can be little doubt that the fruit of *S. amara* is derived from a 2-winged fruit dispersed by wind, which, by the stiffening and lignification of the 2 wings, has been adapted for sea-travel. The distribution of the few species of the genus suggests that it is a dying one, and the only species with anything like a wide distribution is a sea-dispersed one.

Samadera indica is a shrub or treelet which grows among Mangroves in tidal swamps. The fruit, on a long pendulous peduncle, is a leathery indehiscent 1-seeded drupe, narrowly winged, 3 inches long, 2 inches wide, oval and flat. It forms one of from 1 to 5 carpels of a flower. The seed does not completely fill the carpel, and it probably floats from the buoyancy so caused. The plant is, however, scarce in most places, and there are but few observations on its habit recorded. It is found in South India, Ceylon, Mergui, Burma, Johor, Borneo, Labuan, Gebeh, Sumatra, Siberut Island, Amboina, Philippines and Solomon Islands.

Suriana maritima, a seashore shrub or small tree, much of the habit of *Pemphis*. The flowers have 5 small indehiscent 1-seeded carpels, or nucules, about 3 mm. long and broadly conical. The plant, though absent from many spots, occurs almost all over the tropical seashores in both worlds. It grows on sandy beaches and on coral reefs, just above high tide. It is found on the coasts of East Africa, Mozambique, Europa Island, Mauritius, Seychelles, Aldabra, Rodriguez, Diego Garcia (Chagos), Laccadives, Ceylon, Andamans, Nicobars, Minikoi, Cocos-Keeling, Timor Laut, New Guinea, New Caledonia, islands off the Australian coast, Phoenix, Tuamotus, Friendly, Tonga and many other Polynesian Islands, Florida, Holbox and Mugeres Isle, Honduras Bay, West Indies, Bermudas, Bahia and Ceara in Brazil, Margarita Island off Venezuela.

This plant is more remarkable, in its distribution, from the places in which

it does not occur than from those where it does. It is absent from West Africa, India, the Malay Peninsula, Hawaii and western South America, Fiji and Samoa, and Christmas Island. It habitually grows on sandy shores, but in the Bermudas and Bahamas on coastal rocks. Guppy accounts for its absence in some of the spots mentioned by its being destroyed as firewood by wandering islanders or others. This seems to me improbable. *Pemphis acidula*, a plant of similar habit and locality, is not so destroyed. It could not have been exterminated in this way in Christmas Island or the Malay Peninsula.

The floating power of the nucules is due to an unfilled space in the cavity of the nucule; neither the shell nor kernel has any buoyancy of itself. Schimper, who ascertained this, kept nucules afloat for 148 days. Guppy, in Jamaica, had them floating for 7 weeks, and in Turk's Island had 60 floating in sea-water, of which 45 remained on the surface for 9 weeks, while those that sank were nearly all empty husks.

It is therefore certain that these nucules can be dispersed by floating, but, as Guppy says, they can also be carried in floating logs and pumice. Dr. Millspaugh thinks they may be dispersed by attachment in mud to birds' feet, which is possible.

OCHNACEAE.

Brackenridgea.—The fruits of 2 species of this genus, *B. serrulata* and *B. palustris*, were found floating in the lake of Kapuas, in Borneo, by Beccari, and those of another species are recorded by Hemsley as being found floating in the New Guinea sea-drift. The genus is allied to, and has been combined with, *Gomphia* (*Ouratea*), but is perhaps sufficiently distinct. They are shrubs or small trees, of which 2 species, *B. Hookeri* and *B. corymbosa*, occur in the Malay Peninsula and Borneo, 1 species in Queensland, 1 in New Guinea, 1 in the Philippines and 1 in Zanzibar. The fruits, so far as is known, are drupaceous and black, and in most cases at least are dispersed by birds. The seeds, however, contain internal air-spaces which enable them to float, and their distribution suggests that to some extent they have been sea-dispersed. *B. Hookeri*, which is found both in the Malay Peninsula and Borneo, certainly frequents sandy woods near the sea, and its seeds might get into the sea and be so dispersed, but *B. corymbosa* frequents the forested hills of the interior, where it can only be bird-dispersed.

OLACACEAE.

Ximenia americana, a small tree or shrub very widely distributed throughout the tropics of both worlds, partly by sea and partly by pigeons, for the fruit is a yellow drupe. The plant is very abundant and variable inland in tropical Africa, and I suppose this to be its original home; but in other parts of the world it is mainly a seashore plant, and there is no doubt that this form is sea-dispersed. It ranges from West Africa to the Seychelles, South India, Andamans, Ceylon, Malay Peninsula, Java, Amboina, Celebes, Krakatau, Timor, New Guinea, Australia, Polynesia, Florida, West Indies and South America.

The fruits float for months, their buoyancy being due partly to the buoyant kernel aided by a layer of air-bearing tissue inside the shell, as in *Calophyllum inophyllum*.

The wide distribution of the plant is obviously due to its double method of dispersal, primarily by birds and secondarily by river and sea-drift. An inhabitant of dry open land, the plant seems to thrive well on the drier parts of sea-beaches.

MELIACEAE.

Carapa.—No drift seeds are more conspicuous or abundant in the tropical Asiatic seas than the corky, angled, irregular seeds of the 2 common species of *Carapa*, *C. obovata* and *C. moluccensis*. The fruit is a large brown ball, 6 inches or more in diameter, with a leathery pericarp, which breaks up on the tree and releases a number of corky, angled light brown seeds with a testa ½ inch thick. The seeds are 3 or 4 inches long and 2 inches across. They drift away, when fallen into the sea, and are borne in great numbers for long distances, and can be seen abundantly on any beach. They float for many months. The trees grow in tidal forests and Mangrove swamps, and along tidal rivers. Both species occupy approximately the same area. Miquel (Fl. Ind. Bat., i, 346) says that the seeds germinate in the capsule, but neither Guppy, Schimper nor I have ever seen this. *C. obovata* ranges from East Africa and Madagascar, Seychelles, Aldabra, to the Sundribuns, Tenasserim, Andamans, Malay Peninsula, Ceylon, Siam, all the Malay Islands suitable for it, including Krakatau, to Australia and Polynesia; *C. moluccensis*, which is more confined to Mangrove swamps, from the Seychelles and Aldabra to the Andamans, Siam, Cochin China, Malay Peninsula, many of the Malay Islands, including Cocos-Keeling, to Australia and Polynesia.

Guppy points out that the seeds undergo great risks in sea-travelling, from their tendency to germinate in the river before reaching the sea, and from their risk of destruction by boring molluscs and other marine animals, and by the attacks of crabs, or withering of the shoot by the sun on reaching the beaches. He found seeds destroyed by teredo, and on Cocos-Keeling Island, in seeds which had sprouted on the beach, the sprouts were destroyed by crabs or withered by the sun; but the latter are risks which are run by all tidal-swamp plants. They depend entirely on reaching tidal mud after their voyage. Any such seeds thrown up on a coral beach or on a sand-flat must perish, and the same is the case when the seeds of plants growing on sand or coral beach are thrown up on a tidal bank—they also perish. Like seeds of most plants, the greater number perish and the few survive. Guppy points out that the rapid germination on the part of a stranded seed (of tidal trees), though fatal to one stranded on a sandy beach, is a direct advantage to one drifting to the muddy shores of a Mangrove creek, where the germinating seed could at once strike into the mud. This probably is the reason for the rapid germination of tidal seeds.

C. guianensis.—This tree occurs in Eastern South America, Trinidad and West Africa, both inland and on the estuaries. It seems much less of a sea-shore tree than *C. obovata* and *C. moluccensis*, as it grew well in the clay soil of the Botanic Gardens in Singapore, where it was impossible to grow the other species. The seeds resemble those of the truly littoral species, but differ in being smaller, 2 inches long, 1½ inch wide, and 1 inch through in the thickest part, with a thin, brittle, non-corky testa. They are drifted to Jamaica, Tobago and Turk's Island but very few in a germinable condition. As Guppy shows, the passage from America to West Africa by the Gulf Stream, by way of the Azores, would occupy a year, and it may be doubted whether the seeds would arrive in a living condition. *Carapa* is, however, an Old World genus, and might have arrived in America from Africa. The main equatorial current would carry the seeds from the Gulf of Guinea to the coast of Brazil in 3 or 4 months, not much longer than the time required (7 or 8 weeks) for the seeds of *C. moluccensis* to reach Cocos-Keeling Island from Java, 700 miles, as we know they do, in good condition.

The difficulty is actually less than the transition of *Anona*, *Chrysobalanus* and *Symphonia*, and the crossing may be explained by a former land connection.

CELASTRINEAE.

Elaeodendron subrotundum King.—This very widely distributed genus of shrubs or treelets has stony drupes, usually with a more or less succulent pericarp, sometimes red and conspicuous, and doubtless bird-dispersed; but one species, *E. subrotundum*, has flattened dry drupes of a greenish colour, and this plant is the denizen of the tidal rivers and seashores of the Malay Peninsula and Borneo. In section the small fruit has an extremely thin exocarp; the woody hard mesocarp is very large in proportion to the small seed. The fruit is distinctly flattened, so that the section is transversely oval. This is a contrast to the round section, with a fairly thick fleshy exocarp, of such a species as *E. orientale*, which is probably bird-dispersed. *E. subrotundum* is quite common in the south of the Malay Peninsula, and is obviously well adapted for sea-dispersal, yet it has not extended its area further than Borneo.

RHAMNACEAE.

Smythea pacifica, a slender climbing shrub with a flat ovate lanceolate capsule 2 inches long and 1 inch wide, containing a single seed, and dehiscing lengthways into 2 valves. The plant grows in tidal mud of rivers, climbing on trees or bushes. It is allied to *Ventilago*, in which the upper part of the carpels forms a lanceolate wing which does not dehisce, but acts as a flight organ in the wind. The *V. microcarpa*, of Papua, and *Smythea calpicarpa*, of Tenasserim and the Malay Peninsula, seem to be intermediate forms between *S. pacifica* and a typical *Ventilago*, but neither is sea-dispersed. The capsule contains a large empty space above the seed, which is at the base. It will float for months, and Guppy found fruits floating in sea-drift off the Solomon Islands. The plant, though widely distributed, is not very common. It is found in the Malay Peninsula, Borneo, Pulau Sangian, Timor Laut, Philippines, New Guinea and Fiji, and an almost, if not quite, identical one (*S. Dupontii*) grows in the Seychelles. Its habitat in tidal-mud rivers perhaps accounts for its absence in many places. This appears to be another case of the evolution of a sea-dispersed plant from a wind-dispersed one in a way quite distinct from the evolution stories of *Heritiera*, *Melochia*, *Casuarina* and *Dolichandrone Rheedii*.

Colubrina asiatica.—The genus to which this plant belongs is chiefly American. Indeed, excluding *C. travancorica* and *C. anomala*—which have little, if any, affinity with it, and should probably be excluded from the genus—*C. asiatica* is nearly the only species in the Old World, the others being *C. pubescens*, a local variety of it, and *C. pedunculata*, of Christmas Island, probably a local derivative. The ordinary seashore form of *C asiatica* is a shrub about 4 or 5 feet tall, though in some places, with its straggling branches, it is almost tree-like. The capsule contains 3 seeds with rounded backs and acute inner faces. It is round, and the thin pericarp breaks up irregularly. The seeds are very light and float for months, being incompletely filled with the crumpled cotyledons. They are very different from the small flattened polished seeds of *C. ferruginosa*, of Jamaica, which are dispersed by the explosion of the hard cocci, much as in an *Euphorbia*. The plant is found in Polynesia, Cook Islands, Marquesas, etc., Australia, Malay Peninsula and Malay Islands, including Krakatau, Mergui, Andamans, Nicobars, India, Mascarene Islands and East Africa, South China, Bonin Isles and Formosa. It has appeared recently in Jamaica. Grisebach mentions it there, and it has been found on a beach in North Jamaica, and by Harris on the banks of the Plantain Garden River; it is considered to have been introduced there by Fawcett. It is absent from Hawaii, West Africa and the New World, except in Jamaica as stated, as well

as Cocos-Keeling and Christmas Islands (unless *C. paniculata* is a derivation), and some islands and coasts where it could not grow.

As all its allies are American, I would suggest that it reached Polynesia from America by sea, though it is not known to occur there now. It appears to have been introduced into Jamaica, but whether intentionally or in sand-ballast cannot be said. It is a plant of no use or ornament, but Gamble says (in the "Flora of Madras") that it is sometimes planted in India. It generally grows on sandy places near the sea, but not near enough for the seeds to fall directly into the sea. Apparently they are shed beneath the bush, and washed by rain or blown by wind on to the sea-edge and so drifted away.

AMPELIDEAE.

Vitis.—All the plants in this order are, or can be, bird-dispersed. The seeds of *Vitis vinifera* sink in water, as do fresh and dried fruits. I have seen two strong-growing plants of the common Vine growing in an embankment of the Thames between Barnes Bridge and Hammersmith below very high tide mark. I suppose they were introduced there by human agency, perhaps from seeds dropped by a picnic party. Lefroy (in the "Botany of Bermuda") writes:—"An interesting example of the diffusion of plants was afforded by the foundering "of a ship, *Minnie Breslauer*, Jan. 6, 1873 (off the Bermudas). She had a cargo "of white Lisbon grapes, many of which were washed ashore, and the seeds "germinated at high-water mark. Numbers of plants were taken up, and some "bore fruit in 1876." I have but few records of seeds dispersed by shipwreck, but it is a factor which must be taken into account, as some plants may have been carried thus to remote islets, in comparatively early days, and their presence there might be puzzling.

Vitis trifolia has established itself in Krakatau, *V. repens* and *V. pedata* var. in Christmas Island, but these may have been brought by birds. Guppy found seeds of some species in drift at Cocos-Keeling Island.

Leea sambucina.—A fruit believed to be this, apparently in good condition, was found in the New Guinea sea-drift (Hemsley, Challenger Reports), and a variety of *Leea sambucina* is found in Christmas Island. *L. rubra*, with red fruits, is a tidal-river plant in the Malay Peninsula and Java, and may be distributed along the coast by sea.

SAPINDACEAE.

Sapindus saponaria, the Soap Berry tree, is a native of South America. Guppy points out the occurrence of two endemic species of the genus in Hawaii and Fiji respectively, and *S. saponaria* in Tahiti, Marquesas and Easter Island. He suggests that these seeds, though 1 inch through, might be carried by birds over the 1,500 to 2,000 miles of ocean, as they possess a fleshy mesocarp which might attract them. However, they may have arrived at these islands by sea, for the first plant of *S. saponaria* known in the Bermudas sprang from drift seed, and in 1841 a plant sprang up from a heap of seaweed there. This species, abundant in South America, is found also in Timor Laut, the Philippines, and Galapagos, as well as the Island of Margarita off Venezuela. It is quite possible that the Soap Berry was introduced into the Philippines by the early Jesuits, and fruits may thence have drifted to Timor Laut.

Pometia eximia (*P. pinnata*).—The round woody seeds of this tree have been found in sea-drift in Java, but there is some reason to believe it is sea-dispersed. It is an inland continental tree, often growing in forests by streams, and is found in the Andamans, Ceylon, all Malaya, and Polynesia.

Cardiospermum Halicacabum (Balloon Vine).—The genus has its headquarters

in South America, and this species, also a native of the same country, has spread all over the tropics. It seems to have been partly sea-dispersed, also spread by rivers, and to a considerable extent accidentally and intentionally by man. Its bladdery fruits may also be blown short distances by wind. The plant is found largely in waste ground and near villages, and also on railway banks. In such places it owes its dispersal to man. It is frequently used as a vegetable or medicine, and the stems to make baskets. It is recorded in many places as a river-bank plant, and in such spots the capsule may readily drift along the stream. But as it occurs on many islands, including the shore of Christmas Island, I think it owes part of its distribution to sea-dispersal. The closely allied *C. canescens* (*C. corindum*), a South American plant, is found also in West Africa and Galapagos, and the very distinct *C. grandiflorum* grows both in South America and West Africa.

C. Halicacabum is a wiry climber with a dilated capsule with thin walls and a number of small globose seeds (Pl. IV, fig. 6) Guppy finds these seeds sink at once or within a few days, even after drying for months, and seems inclined to attribute their dispersal to birds. It is common in South America, and is found in most of Africa up to Algeria, Arabia and Muscat, and in the Cape Verde Islands, on coral beaches in Mombasa, Expedition Isle, Zambesi, all the Mascarene Islands and Madagascar, Madras, Andamans, Ceylon, Malay Peninsula (mostly on waste ground), Siam (railway and river banks); most of the Malay Islands, including New Guinea, far up the Utakwa River, Christmas Island seashore (one plant 1904), Australia (chiefly river banks); most of the Polynesian Islands, occurring in Tahiti when visited by Captain Cook (1768-1780), Bermudas. It is absent from Krakatau, Cocos-Keeling and Aldabra.

Dodonaea viscosa.—A genus of some interest is *Dodonaea*, which comprises a number of plants very closely allied, many of which have been accredited to one species, *D. viscosa*. They vary from small shrubs to medium-sized trees. These plants are most abundant on the sandy plains of Australia, which is probably their ancestral home, and whence they spread to Polynesia, and through the Malay region to India and Africa, and to the coasts of the West Indies, and South America. Some of the species are mere shrubs, 2 or 3 feet tall, others are trees of from 30 to 60 feet in height. The fruit is round, about 1 inch wide, the pericarp thin and dilated so as to be bladder-like, and surrounded entirely by a very thin papery wing or, to be more accurate, 2 wings (the keels of the carpels), which meet at both ends. Fruits with 3 wings occur, as in *Ptelea*. Each cell of the 2-celled fruit contains 1 or 2 seeds, and its wall splits between the wings and releases them (Pl. IV, fig. 8).

The most widely-distributed forms are the inhabitants of sand-banks by the sea. Guppy ("Naturalist in the Pacific," p. 338) discusses the dissemination of *Dodonaea* at some length. The light, inflated winged capsules, about 1 inch across, he says, can be blown for long distances in the air by strong winds, but, as is also remarked by Schimper ("Indo-Malayan Strandflora," p. 157), they are much too large to be transported by wind across a broad tract of sea.

Guppy suggests that the capsules, before dehiscing, would not stand the rough-and-tumble of the sea, and has not found them in the shore-drift of Fiji, nor have I seen them floating in the seas of the Malay region. He found that the seeds possess some floating powers, but that in Hawaii only half the seeds floated. Schimper, with well-dried seeds, found that they floated for from 10 to 60 days.

It is possible that Guppy, from whom I gather that the plant in Hawaii is an inland plant, may have experimented with an inland form in which the seeds are losing their floating power. A similar case of two forms of apparently

the same species, with two forms of seeds, one floating and the other not floating, occurs in *Matricaria inodora*, of which the achenes of the land form sink, and those of the seashore form (var. *maritima*) float.

Hillebrand suggests that the glutinous capsules might adhere to birds and so be carried about, but Guppy quite correctly says that the stickiness only occurs in mature capsules, and they are not sticky enough to adhere to the feathers of birds. He suggests, however, that the birds might swallow the capsules and pass the hard seeds.

I do not think it at all probable that birds have played any part in the dispersal of this plant, and it is most improbable that any birds would eat this dry, tasteless capsule.

The plant is absent from most oceanic islands, but reached Krakatau from Java between 1877 and 1906. In the Malay Peninsula the plant, there a dwarf shrub, is always a sea-sand plant and does not occur inland at all, but is dotted along the coasts. I have little doubt that it has travelled over its large area by sea, but spread further along the sand-hills by aid of the wind, as it grows regularly on sandy spots at some distance from the sea-edge, and from the sand-hills the capsules may readily be blown into the sea, where they, or their seeds, may drift on and be stranded further along the coasts.

Guppy, in summing up his notes on these plants, is not inclined to exclude any of the suggested means of dissemination, and puts in order of effectiveness birds, sea-currents, then wind. I should be inclined to exclude birds as agents in dissemination altogether, and put as its original source of dispersal ocean currents, assisted by wind in blowing the capsules into the sea and, after it had been established on the coasts, frequently carrying them inland.

The mountain forms or species in Hawaii and Tahiti are described as bushes or small trees 20 feet high (Nadeaud and Guppy). These I imagine are modified descendants of *D. viscosa*, the seashore shrub, and the same suggestion applies to the tree form of India and Java. In Ceylon, too, it is described as a shrub or small tree in open waste ground in the low country, and ascending to a height of 4,000 feet, rather rare and local, but where it occurs it grows gregariously in great abundance.

These mountain plants may be either descendants of *D. viscosa* which have migrated inland from the sea-coast, or have attained their high position by elevation of the land, and been modified from their environment.

The evolution of the thin light 2-winged fruit of *D. viscosa* therefore resembles that of the winged fruits of *Terminalia* and *Combretum* (*see under* Calycine Winged Fruits, pp. 74 and 102) in having first a heavy angled fruit capable of being blown some distance along the ground, then, by a gradual reduction of the seed-vessel and an accompanying enlargement of the wings, passing into the very light fruit with wide wings reduced in number to two only, which we have seen, in *Ptelea*, can go further in the wind than the winged ones.

ANACARDIACEAE.

Gluta Bengas, a poisonous tree with a brown fleshy drupe, elliptic, occurs on river banks, and is undoubtedly water-dispersed. It arrived in Krakatau in 1919, but this is the only case I know of its travelling by sea. It is a native of the Malay Peninsula, Java and Sumatra.

G. coarctata, a tidal-river, low bushy tree. Fruits irregularly warted, brown, fleshy, sub-globose, about 2 inches through, very poisonous. This floats in the rivers very abundantly in the Malay Peninsula and Borneo. Greshoff ("Nuttige Indische Planten") quotes from Upwich (Gen. Tydsch. v. Nederl. Ind., xxxiv, 795) an account of two whole companies of a military expedition being affected by serious injuries to the feet from the

fruits of Rengas trees (doubtless *G. coarctata*) in the waters of the rivers they were wading across.

Dracontomelum mangiferum.—This tree often (at all events, in the Malay Peninsula) grows on river banks. Guppy says of *D. vitiense*, the seeds float only a few hours. Hemsley records the occurrence of *Dracontomelum* seed in drift off New Guinea, but dead.

Mangifera indica.—Empty stones of this are found in sea-drift in the West Indies, Australia, and occasionally in Europe. They are evidently all from waste fruit or stones thrown overboard from ships.

Anacardium occidentale (Cashew Nut).—This tree, a native of South America, was introduced into the Old World in the 16th century, Linschoten mentioned it as occurring in Malacca in 1583, but Garcia da Orta, in 1593, only knew of it in Brazil. It was cultivated by the Jesuit missionaries for the swollen juicy peduncle of the fruit, as well as for the seeds (Cashew nuts). It is now common on sandy shores in the Malay Peninsula and elsewhere, and seems to have reverted to the wild form with uneatable peduncle. The Malays and others occasionally eat the kernels, but it is no longer cultivated in Asia. The fruit, on the end of the fleshy peduncle, is kidney-shaped and contains 1 seed. It is absent from Australia and Polynesia and all distant islands. The fruits, detached from the peduncle, are certainly to some extent drifted along the sea-coasts, but it evidently cannot float far safely. J. Flygare (in Amoen. Acad. Linn., viii, 3, 1768) says that seeds of this plant, with those of *Cassia fistula*, *Mimosa* (*Entada*) *scandens* and Coco-nuts, have been thrown up on the Norway coasts, and the seeds have germinated successfully. They do not seem to have occurred since, and as Coco-nuts are also unrecorded as recent European drift fruits, it is possible that these may have come from a shipwreck.

Spondias dulcis, a big tree with drupes of large size, floats readily in the sea. It occurred in Christmas Island, but here probably brought by some large bird. *S. lutea* is a similar tree, wild and cultivated in South America, West Indies and west coast of Africa. The stones of the drupes are provided with a corky covering possessing great buoyancy, and they are common in river- and sea-drift (Guppy). Guppy found them in the floating drift of the river at Guayaquil, and Pacific and Atlantic coasts of the Panama Isthmus. *S. mangifera* occurred in Krakatau, no doubt sea-drifted, and also in Little Coco (Andamans). *S. purpurea* occurs in Fernando de Noronha; possibly a human introduction, but also dispersed by birds. It may, however, have arrived by sea.

LEGUMINOSAE.

Lathyrus maritimus, the Sea-Pea, grows on sand or shingle on our coasts, as well as in many parts of the world. The seeds are dispersed by sea. They are round and brownish-grey, ¼ inch through. The testa is very thin, though rather hard, and is buoyant, but the main buoyancy is due to the very light cotyledons which completely fill the testa. Sernander states they were found in quantities by J. Schmidt, cast up on sand islets near Falster, in Denmark. Norman says it is distributed all over the coasts of Arctic America through the agency of currents. Guppy writes:—" Some small leguminous seeds, " seemingly of this species, which I found in the beach-drift of Woolacombe " Sands, in Devonshire, floated uninjured in sea-water for many weeks." However, the plant does not seem to occur anywhere now on the coast of western England.

It is one of the most widely distributed species of any in the genus, only excelled by a few fodder plants which have been intentionally or accidentally carried about the globe by man. It is found on the coasts of Europe, Kams-

chatka, China and Japan, Labrador, Newfoundland, Mexico and temperate South America, but is absent from the Canaries, Azores and Madeira. It does not appear to be abundant anywhere.

Vigna is a tropical genus of creeping or climbing yellow-flowered Vetches, of which several species are littoral and very widely diffused. *Vigna lutea* (*V. marina*, *V. retusa*) is a common seashore plant on sandy or pebbly shores throughout the tropics of the Old World. It is found in South Africa, India, Ceylon, the Andamans, on the islands off the Tenasserim coast, Malay Peninsula and the little island Pulau Redang on the east coast; Borneo, Sumatra, Sipora Island, Celebes, Amboina, Philippines, New Guinea, Krakatau, Formosa, Harbour Island, Kelung, China, Australia on Dunk Island, Moreton Isle, Hawick group, Admiralty, New Hebrides, Solomon Isles, Cook Isles, Polynesia. It seems very characteristic of islands.

According to Guppy, the buoyancy of the seeds is due to a large central cavity between the cotyledons, as in *Entada* and *Mucuna*. The small oblong bean has a very hard testa which floats of itself, and I find also an unusually large air-space between the cotyledons, but the cotyledons themselves are non-buoyant. *V. luteola* is a similar plant which is rather more widely spread, as it not only occurs in Asia, India in the Sundribuns, Siam in ditches and moats, Philippines, Krakatau and Australia, but also in Florida, the West Indies, South America and the Galapagos Islands.

Desmodium umbellatum, a seashore shrub about 6 feet tall. The pods, as in all the genus, are flattened and jointed. Each joint, 4 or 5 in number, very woody in this plant and about ¼ inch long, contains a seed and is indehiscent. This seed only partially fills the joint, and the pod is probably also buoyant. It grows in tidal mud and sandy soil in Bombay, Siam, Cochin China, Malay Peninsula, Andamans, Maldives, Ceylon, Sipora Island, Sumatra, most Malay islands, Krakatau, Australia, Polynesia, Mascarene Islands, Zanzibar.

Canavalia.—This is a genus of world-wide Beans, almost entirely seashore plants. Two or more grow exclusively creeping along the sand-hills by the sea; the others usually climb on bushes or trees just behind the sand-banks. Two species, *C. ensiformis* and *C. gladiata* (the Sword Beans) are only known in cultivation, and are doubtless, as Dunn suggests, cultivated forms of one of the wild seashore beans. A few species appear to occur in inland situations, but these may have been carried there, in some cases at least, by human agency; the greater number of species are littoral, and especially island plants. The most widely spread is *C. rosea* (*C. obtusifolia* D.C.), a handsome trailing plant on sand-banks close to the sea. It has large cartilaginous pods with a few rather large beans, which are very light owing to their spongy cotyledons (Guppy), and float unharmed for a very long period in the sea. The plant occurs on sand-banks on the African coasts, both east and west, Mascarene Islands, Siam, Malay Peninsula and Archipelago, North Australia, Kermadec Islands and Meyer Island off New Zealand, Howes Island, Cocos-Keeling, Krakatau, and most of the Polynesian Islands. It did not occur on Christmas Island, simply because there was no sand for it to grow on, but seeds were found in the sea-drift.

In India and Ceylon it is replaced by *C. podocarpa* Dunn, and in the Sino-Japanese region by *C. lineata*, closely allied plants, probably derived from it. In the New World *C. rosea* is found on the seashores of Florida, the West Indies and South America, Cocos Islands, and Fernando de Noronha.

The beans have been found constantly floating in the sea off New Guinea (Moseley, "Botany of Challenger," xiv), in the estuary of the Rewa River, Fiji, and abundantly in the drift of the Fiji and Ecuador beaches (Guppy), off Cocos-Keeling (Ross), and off Christmas Island by myself.

Guppy found them very fickle in their floating powers when experimenting

with them in Fiji. As a rule, 10 per cent. sank at once in sea-water, 50 per cent. floated after 3 weeks, and 10 per cent. over 12 weeks. Of such seeds kept for 3 years, 50 per cent. floated after 11 weeks. This rather suggests that they float best when dry. The sand-banks on which the plants grow are well above high water and very hot, so that the beans become quite dry before either a heavy rain-wash carries them down to the tide-marks, or a heavy storm washes them down into the sea.

C. turgida.—This species differs from *C. rosea* in being a climber on bushes, rocks, or small trees on the sea-coasts. It is nearly as far-dispersed as *C. rosea* is in the Old World, being absent only from the African continent, but it is also absent from the New World. Its furthest point west is the Seychelles, and it ranges from the Bengal coast, Andamans, Burma, Malay Peninsula coasts, and Pulau Redang, Pulau Buru, Pulau Ubin, Malay Islands, to Papua and the Philippines, Christmas Island and Polynesia.

C. turgida is distinguished from all other species (as Prain points out) by its separable endocarp, which closely invests the seeds, and possibly aids in their dispersal in a living state by sea-currents. That it is not so abundant and widely diffused as *C. rosea* is, to some extent at least, I think, due to its requiring trees or bushes to grow on—that is to say, it must be thrown up further by the waves. In Christmas Island the immense waves which strike the island at certain seasons would throw the beans easily on to the rocks and bushes on which I found it growing.

Other species of *Canavalia* growing on remote islands are *C. virosa*, rather an inland species, India, Siam, Africa and Mascarene Islands, occurring in Socotra; and *C. Baueriana* in Norfolk and Cook Islands. In fact, there are few islands in the tropics which do not contain one or other of the species, and those without *Canavalia* seem to be islands unsuited for the growth of the common species *C. rosea* and *C. turgida*.

Erythrina, big trees with narrow pods containing from one to several usually red, small beans. Many are inland species, generally in rather dry open country, and several are typically sea-coast trees growing in sandy or rocky open spots. They are distributed all over the tropics, but several species are carried about by man, being planted for their ornamental scarlet or orange flowers, and at one time largely for shade trees for Cocoa and such plants, or for training Vanilla and Pepper vines on. The seeds float readily and are common in sea-drifts.

The two most widely distributed species are *E. indica* and *E. ovalifolia*, both of which have been widely cultivated by man, the latter especially as a shade for Coffee and Cocoa. It frequently persists a long time after an abandoned estate has been grown over by forest, and may thus appear indigenous. I have seen it thus in the Malay Peninsula, where I think it is not a native plant. But if we cannot be certain as to the origin of these plants on mainlands, we have very good evidence that *Erythrinas* are largely sea-dispersed in their occurrence on islands, and their seeds in sea-drift. Indeed, almost every tropical island where these plants could grow contains one or more species.

E. indica, widely distributed over Asia, and often cultivated, is found in India, Ceylon, Malay Peninsula (wild), and the Malay Islands. It has arrived by sea-drift in Christmas Island, Cocos-Keeling, Krakatau, New Caledonia, Polynesia, Madagascar, Seychelles, Rodriguez.

E. ovalifolia.—Andamans, Ceylon, Krakatau, Samoa, Comoro Islands, New Caledonia. Sprague (in *Kew Bull.*, 1909, p. 198) records the recent appearance of this tree on Pemba, East Africa.

E. aurantiaca and *E.* sp., endemic in Fernando de Noronha. *E. insularis*, endemic, Turtle Island off Australia. *E. velutina*, Galapagos, also South America and West Indies.

The buoyancy of the seeds is due to the lightness of the kernel, as in *Strongylodon*, *Canavalia*, etc. Guppy notes the absence of the littoral *Erythrina indica* in Hawaii, though an inland endemic species occurs, and suggests that the littoral species originally arriving at Hawaii might have been destroyed by insects, and the endemic species derived from it.

Strongylodon ruber (*S. lucidum*) is a climber with oblong pods, usually 1-seeded, the seed rather large, black, 1 inch through, with a red wing-like caruncle. What appears to be this species is found in the Andamans, Ceylon, Christmas Island, Cocos-Keeling Island (seeds in drift), Papua, Philippines, New Caledonia, Australia, Fiji, Hawaii.

There are other species of the genus in the Philippines and Madagascar. It is remarkable that this plant is practically confined to island coasts, and has apparently drifted from Polynesia along the southern edge of Asia. Guppy says the seeds can float for a year and retain their germinating capacity. They are as hard as pebbles, but some of them begin to swell in sea-water in a few days, and come to an end by abortive germination. Out of 5 seeds in water of a temperature between 75° and 90° Fahr., 1 swelled and sank in 10 days, another after 2 months, and 3, of which 1 germinated, floated for over 12 months. The floating power is due to the buoyancy of the kernel.

Mucuna, a genus of climbing plants occurring all over the tropics, of which several species are certainly sea-dispersed. The large, round hard seeds, known as Horse-Eye or Donkey-Eye Beans, are enclosed in a pod covered with very irritating hairs (Cow-hage or Cow-itch). Some of the species have been more or less dispersed by human agency, the young pods being eaten.

One of the most commonly sea-dispersed species is the littoral *M. gigantea*, which scrambles over bushes on the sea-coasts of Asia, and is found in the following islands:—Andamans, Little Coco, Chaungke Island (Burma), Siamese East Coast Islands, Pulau Tengah, Adang Group off Malay Peninsula, Java, Siberut Island off West Sumatra, Karimun Islands, Amboina, Papua, Moreton Bay Islands (Australia), Norfolk Isle, Howes Isle, Cook Isle, Bonin, Tonga, Admiralty, Solomon, Polynesian Isles, Seychelles, Rodriguez, Bourbon. The seeds in this species are round, like those of *M. urens*.

M. macrocarpa is an Indian species absent from the Malayan Islands and Ceylon. Seeds of this were found by Guppy on Cocos-Keeling Island. It is remarkable that (if the identification is correct) the plant has not appeared between India and Cocos-Keeling Island.

M. urens.—This species is found in the West Indies, South America, and tropical Africa. I found seeds washed up on Fernando de Noronha. This is undoubtedly the species of which the beans are found on the Scandinavian coasts (Sernander), brought by the Gulf Stream. The beans are quite round, brown, with a circular black hilum nearly surrounding the seed, which is 1 inch across and about ½ inch thick. Guppy gives this plant as Polynesian, but I have seen no specimen from there, and the plant he refers to must be *M. gigantea*, which is common there.

M. pruriens has a long narrow pod with bean-shaped seeds ½ inch long, black, with a caruncle. This plant occurs in India, Andamans, the Malay Peninsula, Java, Philippines, Krakatau, Wetter, Timor Laut, also in South America and the West Indies, but perhaps only introduced there, as I think it is in the Malay Peninsula, the young beans being used as a vegetable, and the plant usually found in the villages.

According to Guppy, the seeds of *M. urens* owe their buoyancy to a large cavity between the cotyledons, as in *Vigna*, *Entada* and *Guilandina bonducella*. In *M. gigantea* the buoyant tissue forms a layer inside the hard testa of the seed. He says he kept 10 seeds of *M. urens* (this was probably *M. gigantea*) in sea-water in Hawaii for 4½ months floating, the temperature being from

76° to 77°, rarely to 80° Fahr.; but 4 years later, in England, in water at the temperature of between 75° to 90°, 3 of the seeds began to swell out in 10 days and germinated healthily. The other 2 were floating at the end of 12 months, and when planted germinated 1 month later.

Of seeds of *M. macrocarpa* brought from Cocos-Keeling Island, placed in sea-water in England 18 months later, 2 sank after floating from 60 to 100 days, while those of *M. gigantea*, from the same place, all swelled and sank in 8 days. The comparatively rapid sinking of *M. macrocarpa* is curious. The plant is not known to occur in Java or in any of the Malay Islands, but is confined to India, so that the distance the seeds must have travelled to Cocos-Keeling Island must have been very nearly 3,000 miles. Still, it is possible that the previous travels of these, picked up in the Cocos-Keeling drift, had affected their further floating properties, as they could not thus have floated there in the time.

All through the records of distance-floating, however, we notice that there is often a considerable variation in the time that seeds of the same species, and even of the same gathering, float.

Dioclea is a genus of climbing beans of which the headquarters are in South America, where there are numerous species, although 2 of them have been widely disseminated by sea to other parts of the world. The seeds float readily in river and sea for long periods. They are round in shape and flattened, 1 inch long and as wide, and about ½ inch thick, and much resemble those of *Mucuna*. Guppy writes of *D. violacea*, a native of America and the Polynesian Islands, that the seeds floated for 12 months, 1 only sank after 10 months' flotation, and that, like the beans of *Canavalia* and *Strongylodon*, the cause of their buoyancy is the lightness of the kernel (the cotyledons).

Schimper, speaking of *D. reflexa*, says that, when divested of their outer coat, the seeds absorb water and sink, which shows that it is the outer waterproof coat which prevents them from germinating too soon in the water.

Three species of these beautiful plants call for our attention as sea-dispersed plants, *D. reflexa*, *D. violacea* and *D. megacarpa*.

D. reflexa is far the most widely dispersed species of all in the genus, and is the only one which is found in tropical Africa and Asia, as well as South America. It is, curiously (so far as I have seen), not a shore plant, but haunts river banks above tidal water. It climbs on bushes and trees, and has large spikes of violet flowers and big pods containing from 1 to 3 seeds. Though it does not grow on the seashore, the Malays call it Kachang Laut (i.e., Sea-Bean), possibly from their finding the beans floating at sea in their travels.

It is found in West Tropical Africa and Madagascar, in India, in Silhet and Cachar, Ceylon, the Andamans, Malay Peninsula, Borneo, Java and the Philippines, New Guinea and the eastern side of South America. The seeds have been found cast up by the Gulf Stream on the Orkneys and Shetlands in good condition. It is absent from many islands in these areas, and from Australia and Polynesia. The author of the " Flora Braziliensis " suggests that it has been introduced into the Philippine Islands by man, but in view of its wide distribution by sea-travel to other islands in the Malay Archipelago, I do not think that this has been the case. Gaudichaud found abundance of its seeds floating in the sea off Radack, and Hemsley records them as found in sea-drift off New Guinea and on the shores of Tristan d'Acunha, and beans of some species on the Solomon Islands, but these may have been those of *D. violacea*. Its absence in many localities in Asia and Africa is due doubtless to its failure to find any suitable river at the spot where its seeds have been drifted by sea-currents to West Africa, and thence south to Madagascar, and by Ceylon to the Malay Peninsula and islands, as far as the Philippine Islands, where its travels ceased.

D. violacea is a similar plant to *D. reflexa*, and is also an inhabitant of South

America, but, so far as I have seen, only on the east coast. It has also reached the Fiji Islands and Hawaii. It is one of the few plants which have reached these islands from America, the greater part of the Polynesian flora being of Malayan origin. It is remarkable, too, that it seems quite absent from the west coast of America, the nearest point to the Hawaiian Islands. It seems very improbable that the seeds can have reached those islands by drifting round Cape Horn, and its distribution seems to suggest the former existence of open sea between North and South America, as do some other plants mentioned elsewhere (*see* p. 246). It is interesting to note how these beans have migrated from South America in two directions, one easterly to the Old World, and the other westerly to the Polynesian Islands.

D. megacarpa, which is also a Brazilian species, has reached Trinidad, and has been found growing there, and also its beans are found in the sea-drift off the island, but it has not migrated further.

Dalbergia torta (*D. monosperma*), a seashore woody climber, with curved 1-seeded flattened pods about 1 inch long, which do not dehisce. The walls of the pod are rather thick and stiff, of a dark brown colour. In fact, they somewhat resemble those of *Drepanocarpus*, of South America. The seed does not fill the pod completely, but leaves an air-space which suffices to float it. The plant grows climbing over Mangrove trees and in the woods by the sea-shores. It ranges from Bombay and Madras to the Andamans, Cochin China, the Malay Peninsula and islands, to Australia and Fiji. Guppy found its pods floating in the Rewa estuary in Fiji. It is missing from many localities on its route, perhaps because it requires tidal mud and Mangroves for its habitat.

Derris is a large genus of climbers with a few trees inhabiting the forests of tropical Asia. They usually possess thin pods containing from 1 to about 6 seeds, and are mostly wind-dispersed. *D. sinuata* is an inhabitant of tidal river banks, with a pod from 4 to 8 inches long and 1½ inches wide, quite thin, and containing from 1 to 4 seeds. Unlike any other species, the pod is sinuate, with deep indentations between the seeds, so that it eventually breaks up into joints, each containing 1 seed. It does not dehisce, but the segments float away on the current. The plant occurs in Ceylon, Little Coco, Burma, Indo-China, the Malay Peninsula and Borneo. *D. uliginosa* is a regular seashore plant climbing on small trees in sandy or muddy places, well above high tide. The pods are 1-seeded and rounded, from 1 to 2 inches long and about as wide; the seed is flat, round and thin, about 1 inch across. They do not completely fill the rather leathery pod, and are very light, so that they float readily in tidal rivers or the sea. Not only is there a considerable air-space between the seed and the pod, but there is also a space between the cotyledons, as in *Entada*, so that the seed itself can float. Their period of flotation is several months. The plant is very widely distributed, ranging from East Africa, Zanzibar and Delagoa Bay, Natal, Madagascar, Seychelles, to India (both coasts), Andamans, Malay Peninsula and islands, including Krakatau, Aru, Siberut Island, West Sumatra, New Guinea, Australia, New Caledonia, Solomon Islands, Fiji and many other Polynesian Islands.

Pongamia glabra.—This is a small or medium-sized tree abundant on Asiatic sea-coasts. The pods are stiffly leathery or almost woody, oblong, slightly swollen, 1-seeded and indehiscent. The ovary is 2-ovuled, but only 1 seed develops. The fruit is light brown, 1½ to 2 inches long and from ¾ inch to 1 inch wide. The seed only partly fills the cavity of the pod, leaving a space, and the woody carpel is also buoyant (Guppy). The pods float for months, and it has a very wide dispersal area. The tree is found in the Mascarene Islands, Ceylon, South India, Bengal, the Nicobars, Andamans, Mergui, Malay Peninsula, Sumatra, Java, Christmas Island, Krakatau, Timor, Little Kei, Timor Laut,

Hongkong, Bonin, Liukiu, Australia, Fitzroy Island, Cape York, New Caledonia, Solomon Isles, New Hebrides, Fiji.

Gaudichaud records finding its fruits in sea-drift off Radack. Its habitat is rather dry sandy spots usually, but in Christmas Island it grows on the coral rocks.

Sophora.—This is rather a large genus of trees and shrubs, widely spread in the north and south temperate zones, as well as in warmer spots in Africa and Asia. Most of the plants are inhabitants of inland localities, but 2 or 3 are littoral, and 1 of these seashore plants inhabits tropical coasts.

S. tomentosa is a dwarf shrub, handsome, with its bright yellow flowers and long moniliform pods containing from 6 to 8 round black seeds in as many joints of the pod, separated by a short stalk (stipes). The joints do not become detached, but the pod splits for its whole length gradually, and lets the seeds escape one by one. The plant is found on sand-banks by the sea, commonly on islands in both hemispheres. It occurs on the east coasts of Africa, Madagascar, Seychelles, Aldabra, Andamans, Ceylon, Burma, Malay Peninsula, Pulau Adang, Lankawi Islands, and most islands of the Malay Archipelago, including Krakatau, Timor Laut, Aru, etc., to Australia, New Caledonia, Solomon Islands, Fiji, and Cook Isles. It is absent from Hawaii, Cocos-Keeling and Christmas Islands, and in some other places where there are no sandy beaches for it to grow on. The buoyancy of its seeds is due to the light kernels, as in *Canavalia* and *Erythrina*. They can float for 1 year and probably longer. Guppy found that of fresh seeds four-fifths of the number floated for 3 months, and of seeds kept for 3 years half floated after 12 months and remained sound.

S. occidentalis.—This plant much resembles *S. tomentosa* and is evidently nearly allied to it. Indeed, it has been long confused with it. Mr. Hutchinson points out that it is specificially distinct in several points, as indeed Linnaeus noted. It replaces *S. tomentosa* on the west coast of Africa, and Florida, Honduras, the West Indies, and South America.

This is another remarkable instance of the difference between the seashore plants of the east and west coasts of Africa, and of the connection of the West African littoral flora with that of the opposite coast of America.

S. tetraptera.—This is a very different style of plant from *S. tomentosa.* A shrub or small tree with large flowers, and a pod from 3 to 6 inches long, moniliform and winged, with small peas about $\frac{1}{8}$ inch long. It inhabits the Antarctic region, New Zealand, Lord Howe's Island, temperate South America, and Australia. Closely allied to it, and probably mere local forms, are the plants known as *S. microphylla* of South America, Australia, Easter Island and Gough Island, near Tristan d'Acunha, *S. chrysophylla* of Hawaii, *S. Fernandeziana* of Juan Fernandez, and *S. Masafuerana* of Masafuera, Toromiro and Easter Island.

S. chrysophylla inhabits the mountains of Hawaii, and Guppy says that the pods float from between 1 and 2 weeks in sea-water, but, being brittle, break up. The seeds are not buoyant, and do not float at all. It seems likely that the plant is an evolution of the more typical sea-dispersed form, adapted for inland habitation.

S. tetraptera, typical from the coast of Chile. Guppy found that the pods of this break up in from 10 to 14 days in sea-water, but naturally they break up on the tree, and could not therefore fall whole into the sea. Fresh seed floated for 1 month, and of 10 seeds kept for 1 year, 6 floated after 4 months, and of these, 2 germinated in soil. Considering the long-distance distribution of the plant to Easter Island and to Gough Island, Juan Fernandez, etc., it seems probable that the seeds occasionally possess a better buoyancy than this.

Guppy writes at some length on the fact that the mountain species, *S. chrysophylla*, has pods which float for so short a time, and seeds which sink,

the difficulty being to account for its presence in Hawaii. Of *S. tetraptera* he finds seeds in beach-drift at Bahia, San Vincente, 200 miles further north than the plant at Corral, in Chile. He first suggests the derivation of *S. chrysophylla* from a seashore plant like *S. tetraptera*, which is clearly sea-dispersed. He has observed that while in other plants coast-line forms have floating seeds, those forms which live inland have non-buoyant seeds, and cites *Caesalpinia* (*Guilandina*) *bonducella* and *Afzelia bijuga* as examples. This seems a very probable solution. His objection to this theory is that the other Antarctic elements in Hawaii are bird-dispersed, and therefore suggests that this plant must have been bird-carried to the island, and he mentions a Finch (*Loxioides*) and the *Drepanidae* as eating the seeds of this plant. But these birds destroy the seeds in eating. They are not likely to have carried them immense distances internally in safety, and I know of no certain instance of seed-eating birds carrying dry beans like this to so great a distance. He states that wild pigs and sheep feed on the pods, and so the seeds are diffused in the island.

In Gough Island *S. tetraptera* does not occur on the seashore, but inland at some distance from the sea. I would suggest that in this case the tree originally was brought by sea-drifted seeds, and it had gradually made its way up to the inland station, disappearing on the coast and in the intervening land. There is, however, always the possibility of seeds floating in the sea having been picked up by sea-birds and regurgitated on the inland hills.

Ecastophyllum Brownei.—This is a prostrate or climbing shrub, or small tree growing to a height of 40 feet, and inhabiting the seashores of Florida, the West Indies and South America, and also found in West Africa, Fernando Po, and San Thomé Islands. The pod is about 1 inch long, flat, obliquely oblong and 1-seeded. It is undoubtedly dispersed along the river banks by water in South America. Guppy ("Plants, Seeds and Currents," p. 207) states that he found the plant growing in Jamaica and Colon, and its pods were a frequent constituent of the beach-drift. He says the pods float buoyantly when dry, but owe their buoyancy to the air-bearing tissue in the pod. The seed fills the cavity, and is not buoyant. The walls of the pod, however, are too thin and fragile to sustain a long flotation. They showed no tendency to sink after floating for a month, but in some cases the water had penetrated and the seed was decaying. Morris found pods with apparently quite sound seed in the beach-drift of Jamaica ("Chall. Bot.," iv, 300). The tree does not occur in the Bermudas, but that may be due to unsuitable environment. The question arises, how did it get to West Africa? Alp. De Candolle regarded it as naturalised there, but this is very improbable, as there is no reason to imagine anyone taking it across, and it appears to be very abundant, and with *Chrysobalanus* form the jungle on the banks of the River Nun. Guppy urges that it is not possible for the pods to have travelled safely by sea to West Africa. It must be classed with two other tidal-mud plants common to both the African and the American coasts, which have not been carried across in recent times—*Chrysobalanus* and *Drepanocarpus*. I consider this question later under the account of these species (p. 279). It is clear, anyhow, that *Ecastophyllum* has travelled by sea along the American coasts.

Drepanocarpus lunatus.—This tree has a 1-seeded pod curved into a semicircle, flat, and about 1 inch long. It inhabits tidal swamps and especially Mangrove forests, and has just the same distribution as *Ecastophyllum Brownei*, being found in South America from Mexico to Brazil, in Haiti, St. Vincent, and San Lucia, and also in West Africa, in Guinea and Senegal. The pods (save for 1 empty one) have not been found by Guppy or Morris in any beach-drift, and it certainly seems improbable that they could have reached Africa by sea-currents.

These two plants must be classed under the category of *Chrysophyllum*,

Symphonia and *Andira inermis*, a set of river-bank tidal swamp plants which, though possessing no facilities for wide sea-dispersion, are found both on the sea-coasts of America and Africa. *Anona palustris*, growing in the same localities, has been mentioned. Its seeds may have been transported by sea from America to Africa. This possibility, however, appears to be doubtful in the case of the above-mentioned plants, if the distance apart of the two coasts was always as great as it is at present. In fact, the occurrence of these plants on both sides of the Atlantic seems to suggest a close approach or a continuous land connection between the two continents formerly.

Andira inermis (*A. jamaicensis*).—This tree, as mentioned under *Drepanocarpus*, is distributed over Central and South America and West Africa. The pod is 1-seeded, indehiscent, 1½ inches long, ovoid-globose, with a loose fibre-ligneous husk from 2·5 to 3 mm. thick. When fresh, Guppy says, they have little or no buoyancy, sinking at once or in a day or two. When dry they are most buoyant, as he found some in the drift on Turk's Island. Some of them contained a seed, but it was hard, discoloured, and not fit for germination. The seed is non-buoyant, and the husk of the fruit must have been the cause of such buoyancy as it possessed. I notice, however, in herbarium specimens that the seed does not fill up the whole space in the pod, and if this is the same in life, this air-space may cause it to float. It is a river-bank plant, but hardly, it appears, a littoral species. As Guppy remarks, if the strong floating fruits of *Saccoglottis* and *Hippomane mancinella* have failed to reach Africa by sea, it is very improbable that *Andira* fruits could have reached there. It appears, however, to be river-dispersed in its own country.

Pterocarpus dalbergioides, the Andamans Redwood or Padauk.—The circular flat-winged 1-seeded pods of this plant seem to be dispersed by sea to some extent, though they are mostly wind-dispersed. The species of the genus are largely seashore trees. According to Rogers (in Troup's " Sylviculture "), the tree appears in alluvial flats, and the pods are quite light enough for water-dispersal, and the Andamans species may have reached the island by sea.

Cassia fistula, the Indian Laburnum, a handsome tree confined in a wild state to the interior of India. It is also stated to be a native of Africa, but I have seen no specimens from that country, except one cultivated one, the other specimen, referred to this species by Bentham from Africa, being a totally distinct plant. The pods, which have long been imported into Europe as a drug, are long and cylindric, and contain numerous small, flat hard seeds separated by partitions. They were first recorded as sea-drift fruits and seeds by J. Flygare (Linn. Amoen. Acad., viii, 1) as drifted to the Norwegian coasts. Martins met with them cast up on the coasts of France, at Montpellier, in sea-drift, and Hemsley records the occurrence of drift-seeds collected on the shores of Jamaica by Morris. As the plant has not established itself anywhere outside the inland area of India, it is naturally very improbable that the fruits and seeds should have been sea-borne to such distant spots. Martins, however (Mem. Soc. Acad. Montpellier, iii, 339, 1856, and Bull. Soc. Bot. Fr., iii, 34, 1856), explains the story of this. He says the fruits, in the case of those drifted up on the shores of Montpellier, were originally imported to Marseilles, and that those in which the seeds rattled, showing that the pulp in the partitions was dried up, and (this being the important medicinal part of the fruit) were valueless for trade, were thrown into the sea as worthless, and must have drifted the 150 kilometres (about 140 miles) to Montpellier, and something of the same kind must have happened on the coasts of Norway and Sweden.

Guppy (" Plants, Seeds and Currents," p. 152) deals at some length with *C. fistula* and *C. grandis*, the latter being a South American species with pods of the same type. He found the pods, or fragments of both, in the drift on the beaches of Turk's Island, where neither grow. Most of the seeds of the

2 species are impermeable to water, and would withstand the penetration of the sea-water into the pods when broken by the waves. Those drifted to Turk's Island could only have drifted a few hundred miles, and more than half the seeds had been killed by the penetration of water, only from 20 to 40 per cent. being hard and sound; and he doubts much that the pods drifted up on the coasts of Europe could have come from the West Indies, and suggests they came from Egypt up the Mediterranean. However, all these suggestions are quite unnecessary. Martins explains the apparition of the fruits with germinable seeds at Montpellier. The other records of stranding in Europe may be accounted for in some such way. It is to be noticed that they were chiefly found on the Norwegian coasts by Strom and Gunnerus in the middle of the 18th century, but we have very few records of a later date. Up to 1860 or 1870 the pods of *Cassia fistula* were commonly to be seen in jars in all chemists' shops, partly as curiosities, partly for use. This has long ceased. The demand for the drug is small, and they are no longer put in windows as an attraction. Hence its disappearance from European coast-drift. It was a very popular drug in the 17th century, and was carried about the world by the Spaniards. Linschoten mentions it as occurring in Malacca with *Papaya*, *Eugenia Jambolana*, and other useful plants from both sides of the world, in 1583. It has long disappeared from there. Sloane (1688–1689) mentions it as introduced to Hispaniola, Cuba and Jamaica by the Spaniards.

Cassia grandis is a native of South America and the West Indies. Its pods appear to be drifted up on the Turk's Island shores as readily and as abundantly as those of *C. fistula*, but it has spread no further.

Cassia nodosa, abundant on the river banks of the Malay Peninsula, and *Cassia javanica*, of Sumatra and Java, have terete pods like those of *Cassia fistula*. The pods doubtless sometimes drift down the rivers, but are not recorded in any sea-drift, and do not extend to remote islands. Indeed, their distribution areas are all limited.

Cassia siamea.—The pods of this tree are flat, and dehisce longitudinally, so that the seeds fall out, and are so dispersed. The tree appeared at Krakatau after the destruction of the vegetation by the eruption, and was possibly introduced by sea-floating seed. It seems to me, however, that it is quite possible the hard seeds of this and of *Albizzia stipulata*, which also appeared, may have persisted unharmed, buried under the showers of ashes, and been brought to the surface again by denudation and then germinated. It is well known that many seeds, especially of *Leguminosae*, can remain a long time buried uninjured. *C. siamea* is a native of Ceylon, Siam and the Malay Peninsula and Java. It is frequently planted for its ornamental yellow flowers, which are also eaten in curries, and this accounts for its appearance in Christmas Island. I have seen no record of its appearing in any other island, nor, indeed, of any other species doing so, unless introduced by man.

Afzelia bijuga.—The genus *Afzelia* comprises a number of trees in Africa and Asia, some gigantic, others comparatively small. In some African species the seed possesses a bright red aril, and these plants are presumably disseminated by birds, but one or two species are widely dispersed by sea-transport, the most freely so disseminated being *A. bijuga*. (*A. retusa*, which is found in the Ganges delta, the Andamans, Siam, and in the tidal river banks of the Malay Peninsula, is probably a form of *A. bijuga*.) This is a medium-sized tree on sea-coasts, with dehiscent pods containing a few flat, round, hard disc-like seeds, which owe their buoyancy to the lightness of the kernel (cotyledons), the testa having no floating power.

The tree ranges from Madagascar and the Seychelles to Diego Garcia (Chagos Archipelago), India, Cochin China and Siam, Malay Peninsula, Pangkor Island, Java to the Philippines and Papua, Fiji and the Solomon Islands. It is

absent from a good many islands and coast localities where it might be expected to occur, but Bourne gives a clue to the possible cause of this by saying that in Diego Garcia the rats eat the seeds and prevent it from spreading. These animals are abundant on nearly all oceanic islands, and together with crabs, which are apt to eat the plumules and radicles of germinating seeds on the shores, probably account largely for the absence of many plants whose seeds are drifted to distant coasts and islands.

Guppy gives an interesting comparison between the floating powers of the inland and the littoral forms of *Afzelia bijuga*. He found that out of 100 seeds of the littoral plant in Fiji, about 70 floated in sea-water. When the density of the water was lessened, the seeds sank at once, and on the removal of the survivors to fresh water, about 47 still remained afloat. Of 100 of the inland form, 79 were heavier than sea-water, 13 would float in sea-water, and 8 or 9 in fresh water. He observed that the inland seeds averaged between $\frac{8}{10}$ and 1 inch in the greatest diameter, from 12 to 16 going to the weight of an ounce; the littoral seeds measured from $\frac{9}{10}$ to 1 inch in width, and only 10 or 11 weighed an ounce. Thus the littoral seeds were larger than those of the inland forests. It is clear that should the seeds of the littoral tree drift to the mouth of a tidal river, a certain proportion could be carried up to where the water was fresh, or only brackish, as far as the tide went, others would sink when the sea-water became diluted, so that the plant would be distributed along the shallow parts of the river, and left there at the fall of the water.

Guppy notes that, common as the seeds of this tree are in the Polynesian Islands, they do not appear in the drift of Krakatau, Cocos-Keeling, or the south of Java. He suggests that perhaps the seeds of the Malayan plant are less buoyant, or that the tree is less frequent, or that the seedlings are soon destroyed by crabs or rats. It certainly is not rare in the tidal rivers of the Malay Peninsula, but not extremely common, and it usually grows in the thicker parts of the tidal forest, where there are no rats and not many crabs. Possibly only those escape which are carried directly up the tidal river to places free of these animals.

The most interesting fact about the plant is the remarkable variation in the buoyancy of the seeds. In some of the plants especially adapted for sea-dispersal, such as *Carapa*, practically all the seeds float, but here we have a plant in which a certain number float, both of the inland and the littoral forms, but a larger proportion in the case of the latter. The buoyancy is due to the kernel only. What the difference between the kernels of the floating and non-floating seeds is, we do not at present know, but it must be something very small, though it makes the complete difference to the area of distribution of the plant.

Inocarpus edulis is a big tree with large, flat, round, fleshy, leathery green pods containing a single large seed, known as the Otaheite Chestnut, and used as food. This seems to be quite a coral island tree, though it also grows in tidal mud. It is indigenous to Polynesia, Fiji, Marquesas, Tonga, Cook Island, Amboina, Borneo, the tidal river at Kuching, Java, Christmas Island, and New Guinea. In a few other places it is found in cultivation, but chiefly in botanic gardens. The only other known species is a native of Brazil and Guiana. The pods are about 5 inches long, 4 inches wide, and 1 inch through. They are indehiscent, and the exocarp is composed of a thin green epicarp, beneath which is a fibrous, almost woody layer from $\frac{1}{4}$ to $\frac{3}{4}$ inch thick; below this is a pithy white mass, at first very thick, but disappearing when the seed is ripe. This leaves a space, which is no doubt the cause of the buoyancy of the seed. On Christmas Island the fruits were rather smaller than those above described, which were from trees in the Singapore Botanic Garden. They were disseminated over the island by small red land-crabs (*Gecarcinus*), which dragged

them to the mouth of their burrows and ate the green husk. I often saw a dozen or so young plants growing in a circle round the mouth of the crab's burrow.

Guppy considered that this tree in the South Pacific group of Polynesian Islands owes most of its dispersal to human agency, and speaks of its home in Malaya; but it is comparatively scarce in the whole Malay region, and is not planted or used for any purpose whatever, in Borneo at least, where it is certainly wild.

In the South Pacific islands it flourishes in low, moist localities and creeks by Mangrove swamps and estuaries. Guppy states that he found the fruits floating in rivers in flood and at sea, but only $\frac{1}{6}$ had sound seeds, and all picked up at sea were empty, and that the pod is not watertight, and soon decays. "Forty "days would probably be the extreme limit for the flotation in sea-water of "a fruit," and he would much doubt that such a fruit would germinate. He accounts for its occurrence (in abundance) in Christmas Island as evidence of a (mythical) early Malay settlement there. We know from history that there was no human settlement there before the present one, and this is confirmed by the total absence of any commonly-cultivated Malay plants or any weeds of cultivation. The fruit is too large to be carried by birds, and there can be no doubt that it has travelled by sea to Christmas Island—probably from Java, and most likely to the Kuching River in Borneo. As the only other species is South American, I should suggest that the genus first migrated (like *Dioclea violacea*) to the Polynesian Islands, and then to Papua, and so up to Java and Borneo. It has not reached the Malay Peninsula. We had trees of it in Singapore Botanic Gardens, but the Javanese coolies did not seem to recognise it, and had no idea the kernel was good to eat, so that it is extremely improbable that it has been carried about by any of the Malay races to any of the Malay islands.

Guilandina (*Caesalpinia*) *Bonduc* and *Bonducella*.—The seeds of these plants are known as Nicker Nuts. They are quite round stony seeds, lead-grey in *Bonducella* and yellowish in *Bonduc*. The plants are very thorny, scrambling bushes, with short, oblong, loose pods covered with spines, and containing 1 or 2 seeds. The seeds are very hard, and float well for a long period in the sea.

G. Bonducella is the most abundant and widespread of the two species. Both plants are typical seashore bushes, usually growing on rocky spots, but are frequently found inland in some countries. To some extent this is due to human agency.

In India, where *Bonducella* is found up to 2,400 feet in the Himalayas, the shrub is used as a hedge plant, and the seeds valued as medicine, and in other countries they are used as beads and as counters in playing games, and for such-like purposes. There is also some evidence that they are dispersed or carried some way inland by sea-birds—boobies and frigate birds—which swallow them and later regurgitate them (*see* Dispersal by Birds p. 488). But the extensive distribution of these plants is due to sea-transport.

Distribution of *G. Bonducella*.—This plant occurs in India, coast and inland, Ceylon, Andamans, Siam, Malay Peninsula and islands, Cocos-Keeling, Christmas Island, Krakatau (seeds washed up but not yet established), Formosa, Hainan, China, Australia, Barnard Isle, Howes Isle, New Caledonia, Polynesia, Florida, Mexico, West Indies, Bermuda and Galapagos, both coasts of Africa, Madagascar, Seychelles, Bird Isles, Rodriguez. Seeds in good condition have also been found washed up in England, Orkney, West Scotland, Ireland, Scandinavia, Faroes, Azores, St. Helena and Tristan d'Acunha. In fact, the seeds have travelled by sea all over the world, and the plant is absent from the rest of the world only on account of the unsuitable climate. Guppy, who gives a very complete account of this plant, says also that in some places it

has failed to establish itself on the seashore because the crabs devour the plumule and radicle as soon as the seed begins to germinate. The seeds are extremely hard, and require the blow of a hammer to break them. The outer coat of the testa is very tough and waterproof, and the seed does not germinate until there is a small incision or rubbing made so as to expose the middle layer of the testa, which at once begins to absorb water, when in a day or two the whole testa becomes quite soft. Then the seed swells up and begins to germinate. Thus the seeds do not germinate when floating, which happens in many floating seeds, and, as Guppy says, restricts their dispersal. I suggest that in these seeds it is the striking against coral rocks or stones on the shores by the beats of the waves that causes the rupture of the hard outer layer of the seed-testa, and permits the water to be absorbed.

Guppy shows that the seeds would keep for 2½ years floating in water, and never show any signs of germination, but when filed and planted, germinated healthily, while those of *Mucuna* and *Strongylodon*, which have a much smaller range of dispersal, germinated and sank when the water they were floating in ranged in temperature from 70° to 90° Fahr. The buoyancy of the seed is shown by him to be mainly due to a large cavity between the cotyledons, and also to a shrinkage of the kernel from the hard outer wall of the seed. Schimper states that buoyant seeds all rattled when shaken, and that the buoyancy is due to the incomplete filling of the testa. Guppy found, however, that the rattling of the seeds was quite exceptional, even in seeds kept for 5 years, and that loose kernels were more frequent with non-buoyant seeds than with buoyant ones.

In Fiji he found of buoyant seeds the proportion of loose kernels was from 17 to 20 per cent., of non-buoyant seeds as much as 60 per cent. In the non-buoyant seeds of Hawaii the central cavity was reduced to a slit or was absent. In the non-buoyant seeds of the inland species of Vanua Levu (Fiji) ⅔ of the seeds had loose kernels with the cotyledons closely appressed together; in the others there was a lateral cavity outside the kernel, and a very narrow slit between the cotyledons.

It is clear from this that, as in *Entada* and other such plants, the space between the 2 cotyledons is the essential element for the buoyancy of the seed, and it will be noticed that what appears to be an insignificant and trivial modification of the kernel is of vast importance to the life of the species. It is, indeed, through this little space between the cotyledons that these plants are distributed over the whole tropical world.

Guilandina Bonduc.—As Hemsley says (" Bot. Chall. Exped.," iii): " This " species has often been confused with the last. It differs in its larger leaflets, " absence of foliaceous stipules, and pale yellowish seeds." Guppy shows that in Fiji there are three strand forms—*Bonduc*, *Bonducella*, and an intermediate. There is also an inland form which has lanceolate (not oblong) leaflets and a pod without prickles. The intermediate form may be a hybrid, as both *Bonduc* and *Bonducella* occur together in Fiji, but he suggests that all may belong to one polymorphic species.

G. Bonduc is not so abundant as *G. Bonducella*, but is nearly as widely distributed. It is found in India, Ceylon, Malay Peninsula, Java, Borneo, Philippines, Cook Island, Norfolk Island, Polynesia, tropical Africa, Florida, West Indies, Panama, New Grenada. Like *Bonducella*, it is usually a coast plant, but in some places, e.g., tropical Africa, it occurs inland, and it goes some way up the rivers at Sarawak and Lundu in Borneo.

Caesalpinia Nuga, a Mangrove swamp climber or tidal-river plant. In Ceylon it is said to reach 3,000 feet altitude. It has a woody, 1-seeded pod slowly dehiscent, which readily floats. Guppy found its seeds in the sea-drift of the Solomon Islands. This is distributed over India, Andamans, Ceylon, Cochin

China, Liukiu islands, Formosa, Hongkong, Malay Peninsula, Borneo, Timor, Timor Laut, Amboina, Buru, Celebes, Papua, Solomon Isles.

I have little information about this plant, the area of distribution of which is rather limited compared with that of *Dioclea*, *Mucuna*, etc., but, being an inhabitant of Mangrove swamps and tidal thickets, it is clear that it is disseminated by sea-transport.

Cynometra ramiflora.—There are two varieties of this tree, one of which, var. *mimosoides*, is a small tree growing in Mangrove swamps and producing rather scantily small 1-seeded, corky oblong fruits about 1 inch long, the pericarp being very thick. They either do not dehisce at all or very tardily, and the fruit falls entire into the sea and is drifted about. It is found in the Sundribuns of India and Travancore, in Ceylon, the Andamans, Burma, Mergui, Cochin China, on Pulau Condor, in the Malay Peninsula and islands as far as Timor Laut. There is a larger form, with bigger leaflets and fruit 2 inches long, which is found in Borneo and Java, and of which the fruits are commonly found in sea-drift on the Malay Archipelago. Mr. Ross gave me specimens of fruit containing seed which had been drifted up on Cocos-Keeling Island. Schimper, who also found fruits in sea-drift off Java, calls the plant *C. cauliflora* in his "Strand-Flora." It is not, however, the true *C. cauliflora*, which is a species only known in cultivation. Prain calls it *C. ramiflora* var. *genuina*, and records it from Java, Ceram and Amboina.

C. grandiflora of Polynesia is allied to *C. inaequalifolia* of the Malay Peninsula and inland forest species, but Guppy states that the pods of the Polynesian plant float.

The areas occupied by the occurrence of *C. ramiflora* and *C. grandiflora* are obviously limited by their being Mangrove swamp plants only, and their dispersal due to the thick, light corky pod.

Entada.—This genus of woody climbers is famous in dispersal for its far-drifted beans, which have long been known to be sea-borne, from tropical America to the Faroe Islands and Iceland, and, picked up on the seashores by the natives, were known as "fairies' kidneys" and such names. The pods are from 2 to 4 feet long and 3 inches wide, woody, with a strong woody suture running the whole length of the pod. The seeds are in separate compartments of the pod, and about 13 to 15 or more in a pod. In dehiscence the walls of the compartments fall away and the seed falls to the ground. They are round and flat, 1½ to 3 inches wide and about ½ of an inch thick, dark brown, polished and hard. (There is a species in the Malay Peninsula to which this description does not apply, *Entada spiralis*, in which the pod is spiral, not woody, and which breaks up into joints, which dehisce and enclose a much larger thick seed with a thin testa. This species is not distributed by water and is very local, occurring only in Malay forests.)

The greater number of species of *Entada* have been classed and spoken of as *Entada scandens* Linn., a mixture of several species quite distinct, so that the idea of one species being practically cosmopolitan in the tropics is erroneous. The Indian and Malayan species are not identical with the American ones; each has its own limit of distribution. It is, however, difficult to separate the species of the *E. scandens* section, as the specimens in most herbaria are poor and incomplete. In the Malay Peninsula *Entada Schefferi* is the most common species, and is not a littoral plant at all. It occurs far inland, climbing on the trees on the banks of rivers, down which its seeds float. Schimper, however, speaks of a species, which is probably this one, occurring in the beach formation in Java. Seeds washed down by river may float to the sea, and it is perhaps seeds of this species which have been drifted up on Cocos-Keeling and Krakatau. I have seen it from the Malay Peninsula and Java, Sumatra, Philippines, Australia and Siam.

Trimen describes the Ceylon plant (*E. Pursaetha*) as found in the low country up to 2,000 feet altitude.

The Fiji species (*E.* sp.) is, according to Seemann, most characteristic of the Mangrove formation. It is also found amongst the trees at the back of the Mangrove swamp, and inland to the border of the forests of the interior. Guppy found it in Vanua Levu, 4 miles inland and at an altitude of 2,400 feet. Reinecke talks of it in Samoa, only in connection with the primeval forest. The species does not seem to have been described botanically. It is distinct from *E. Schefferi* and other species.

In Ecuador and the Panama Isthmus the species is *E. gigalobium*, and Guppy says that this *Entada* grows not only on the coast, but also on the hill slopes in the rear of the Mangrove belt. He adds that it grows in the interior of the Panama Isthmus, and that rivers on the north and south sides now carry the seeds seawards from the same divide to the Atlantic and Pacific oceans. It also occurs in the West Indies and Mexico. It is, I believe, the seeds of this species which are carried by the Gulf Stream to the coasts of Europe, where it appears to be the most abundant and conspicuous of all the Gulf Stream drift-seeds.

Seeds in good condition have been seen drifted from the tropics to the Arctic regions. They are found on the coasts of Jamaica and Turk's Island, Azores, west coast of Ireland, south and west coasts of England, Wales, Scotland, the Hebrides, Orkney Islands, Faroe Islands (" A Description of the Islands and Inhabitants of Faeroe," L. Debes, 1676, transl.), the Norwegian coasts, but most frequently north of the Sundmore district, Nova Zembla, and north coast of France, and have been found in peat bogs of Sweden in a semi-fossil state of post-glacial date (Sernander). There is no record of their having been found fossil at an earlier period, though one might expect them to occur with the now far more local Nipa Palm of the Eocene of Southern England.

Seeds of some species have also been found cast up on the shores of St. Helena, but of which one I do not know—possibly the same one, or perhaps a West African species. The occurrence of these seeds on the seashore has been known to Europeans for many centuries, and they have often been made into snuff-boxes and such things. In spite of the durability and abundance of the seeds, the plant has seldom established itself on distant islands, probably because it rarely reaches a spot where it can successfully grow. The species seem to be typically river-bank plants, and require fairly large trees to grow on.

The buoyancy of the seeds has been studied by Guppy and Schimper. The former made experiments on the floating powers of the Fijian and the Ecuador species, and found that 50 per cent. of the seeds had no buoyancy in sea-water. Of those that can float, from $\frac{1}{3}$ to $\frac{1}{2}$ sink in fresh water, so that only $\frac{1}{4}$ or $\frac{1}{3}$ would be carried down to the sea. Those that will float appear to be able to float indefinitely, and he had one that floated unharmed for a whole year.

I must point out that Guppy, like most botanists, considered the numerous species of this group to be one species only; but as the forms of *Entada* differ in foliage and flowers, as well as often conspicuously in form of fruit and seed, they may well differ in buoyancy also. The different species of *Entada* have not very wide areas of distribution.

Neither the seed-testa nor the kernel have any floating powers; their buoyancy arises from the large central cavity produced by the shrinking and bending outward of the cotyledons during the shrinking and hardening of the maturing seed. With seeds that sink, the cavity is reduced to a small size, and may be only a narrow slit. Where the cotyledons are unusually thick and heavy, even a large cavity will not give buoyancy to the seed.

There is an indication that seeds of inland plants which have ripened in the forests sink in greater proportion than those of littoral plants or those growing on banks of estuaries. There seems to be a tendency for inland species of *Entada* to develop thick cotyledons, for the seed of the entirely inland species, *E. spiralis*, is 1 inch through, with a very thin testa, while those of the river-bank *E. Schefferi* are only ¼ of an inch thick and the testa is thick and hard.

Guppy points out that the drying process which accompanies the setting and ripening of the seed would be less complete, and the cavity between the cotyledons smaller, in seeds ripened in forest shade than in those ripened in more exposed spots. It seems to me also that in seeds falling on a hot sandy beach the cotyledons might be contracted by the heat, so as to leave a larger space between them, and, if these were washed off by a higher rise of tide, would be most likely to float. This suggests, too, that plants growing in hot exposed positions would possess seeds in which the shrinkage of the cotyledons would adapt them for water-dispersal, and at the same time they would be adapted for growth on hot and dry sand-banks, on which they might be floated up, and thus a littoral form or species might be evolved.

Acacia Farnesiana.—This is the most widely-dispersed species of *Acacia* in the world, and its original home has been very variously located. It seems, however, tolerably clear that it originated in Western America, from Texas southward, and has been carried, mainly by man, to various parts of the world in very early days, in spite of the fact that it is not a very valuable economic plant. It is cultivated for the fragrant perfume of its flowers, the fruits are commonly used for making ink, and the tree produces a useful gum. Once in a country, it may be dispersed by cattle, which eat the fruits and disperse the seeds as they do other species of *Acacia*.

It frequents dry sandy spots, not only inland, but often along the sea-coasts. According to Schimper, it haunts the brackish water swamps where the *Nipa* grows, behind the Mangroves in the drier spots in Java. In Jamaica Guppy found it in the loamy soil behind the Mangroves, with such plants as *Hibiscus tiliaceus*. In other places in America it grows abundantly in the arid desert regions, with cacti and yuccas, and this appears to be its natural home, it having later spread to sea-beaches.

But it is with its possible dispersal by sea that we have here to deal, and it may be said at once it has very seldom, if ever, been found in any distant island where it is impossible for it to have been carried by man. Though not rare in Java on the sea-coasts, it is absent from Krakatau and Christmas Island. In Fernando de Noronha it had clearly been introduced, and had spread (perhaps by cattle) to the interior. In Polynesia all the botanists who have dealt with the flora of these islands seem to consider it as not indigenous, but introduced by man. There is no evidence that it was otherwise brought to Madeira, the Cape Verde Islands, and such localities. There remains, however, its occurrence in Cocos-Keeling, where Darwin found it in 1836. He collected there 20 species of plants, including leaf specimens of what is apparently this plant. None of the others are imported weeds of cultivation, but he mentions that besides coconuts, fruit-trees, some other vegetables, and imported grasses occurred there, so that it is quite possible that this may have been introduced from Java by the Malays.

The pods of *Acacia Farnesiana* differ from the majority of those of other species in being fleshy and indehiscent. Guppy found that when green and moist they sank in water, in a few days at most. When dry the pith which fills up the pod dries up, and the pods become black, and the seeds lie loose inside. Of 5 pods put in sea-water, 1 sank in 16 days, 1 in 23 days, and the others within 36 days. The distance that the pods could float would be about 400 miles. The seeds separated sink at once. The pods thus might be floated from one

island to another, if not over 500 miles apart, or along the coasts, and doubtless are thus distributed in some cases, but the 700 miles of sea from Java to Keeling Island would be too far for a pod to cross.

ROSACEAE.

Chrysobalanus Icaco, the Coco Plum, is a shrub common on the coasts of South America from Florida to Brazil, and the West Indies. It has a round pithy plum with a rather hard stone. It grows with *Anona palustris* and *Ecastaphyllum* in tidal mud. The fruit, being pink and showy, might, and probably does, attract pigeons, and it may be so dispersed. Guppy made some observations on the possibility of the transport of this by sea. The stone is ribbed and the walls 2 mm. thick. The seed inside does not fill the cavity, and it is due to this that it floats. The dried fruits lying under the bush are more buoyant than the fresh fruits. Four selected ones floated for 2 months, and of 2 cut open, 1 had a sound seed. He made these experiments because *C. Icaco* is reported to grow on the opposite coast of Africa, and it was desirable to see if the fruit could travel across by sea. The African plant, however, is a distinct species, *C. orbicularis*, and there are 2 or 3 African species, as well as several in South America. The genus is common to both sides of the Atlantic. The distribution of *Icaco*, however, seems to indicate that it is sea-dispersed along the coasts and to the islands of the West Indies. I found a plant suspiciously like it on Fernando de Noronha, in the forests, but it had no fruit and no flowers, so I am not certain of its identification.

RHIZOPHORACEAE.

This order, as at present limited, includes the genera *Rhizophora*, *Ceriops*, *Bruguiera* and *Kandelia*, the characteristic plants of Mangrove swamps, remarkable for their peculiar method of seed-dispersal and the habits of the trees. Other allied trees and shrubs of an inland habitat and a very ordinary method of seed-dispersal often included, *Carallia* and *Anisophyllea*, etc., I exclude from the order, under *Legnotidae* and *Anisophyllaceae*.

As thus limited, the order *Rhizophoraceae* is the only phanerogamic one in which all the species are sea-dispersed.

The plants are all trees or large shrubs which form the extensive areas of Mangrove forests fringing the shores of the tropics wherever the soil of the coasts is suitable. They are practically confined to the mouths of tidal rivers and muddy shores within tide-marks. The forests usually contain few or no other trees or shrubs, though such trees as *Heritiera littoralis* and *Avicennia* occur sometimes mixed with them. The distribution of these trees in the area covered by the order is limited by their soil requirements. Where there is the stiff blue mud that these trees grow in, whether along the edge of the coast or up the tidal rivers, they soon establish themselves. Their long aerial roots, arching into the mud, serve not only to support the tree, but also to detain the drifting silt, so that in time one or two trees may develop into a forest, and the coast-line is gradually increased out to sea.

Some of these forests are very extensive, as in Northern Borneo and on the west coast of the Malay Peninsula. Here the mud is brought down by the denudation of the granite backbone mountain ranges of the interior, and the Mangroves are abundant. On the east coast of the Peninsula the hills are of sandstone, and the result of denudation is a sandy shore, quite unsuitable for the growth of the Mangroves, which are consequently absent, except from the mouths of a few rivers which have brought down mud from the granite hills behind the sandstone range.

The floating seedlings drift to the coral reefs of Cocos-Keeling and Christmas Islands and to the sandy, coral, or pumice shores of Krakatau, but perish, finding no soil suited for their growth. They wander all over the warm parts of the tropical area, and only effect a settlement where there is the mud in which they can grow. Their survival and establishment are dictated by the formation of the mountains of the interior of the land. If these are of granite, or some rock which can disintegrate into a mud-silt, they can establish themselves on the coast; if of sandstone or limestone, the soil formed is useless to them, and they fail to make a settlement.

The Mangroves have two separate areas: one, the largest, extends from Polynesia through the Malay region to Ceylon and Southern India, and up the Malay Peninsula by Burma to the Bay of Bengal, from Ceylon to the Mascarene Islands, touching South Africa, and along the coast of East Africa to Arabia. Another branch radiates from the Malay region up the Chinese coast to Formosa. The other area with a different set of species is found on the coasts of tropical America, as far north as Florida and south to Brazil, and across the Atlantic to the opposite coast of Africa. One of the American species has migrated to Polynesia, where it meets with the Asiatic species. The species of the east coast of America has reached the west coast, but the Asiatic Mangroves have only reached the east coast of Africa, and the West African ones have not yet reached the east coast.

This is not the only case of this distribution of sea-dispersed plants of the two sides of the world. One may say that, though these plants are identical on both coasts of America, they are practically always different on both coasts of Africa. The sea-dispersed plants common to both coasts of Africa are common also to those of America.

The great characteristic of the *Rhizophoraceae* is the germination of the seed in the ovary, which remains attached to the tree till the cylindric, stout radicle has long protruded, which is known as vivipary. The evolution of the plantlets of *Rhizophora* and *Bruguiera* is well described by Guppy ("Notes of a Naturalist," p. 451). The ovary is 2-celled and contains 4 ovules, all but one of which are suppressed, but he records the development of 2 or more, rarely 3, seeds in about 1 per cent. of cases. I do not remember having ever seen a case. After fertilisation it takes 229 days, or nearly 33 weeks, before it is fully developed and the young plant falls off the tree into the water. The fully-developed radicle in *Rhizophora conjugata* is cigar-shaped, with an acute point, green, about 10 or 12 inches long; in R. *mucronata*, 1 to 2 feet long (Pl. XIV).

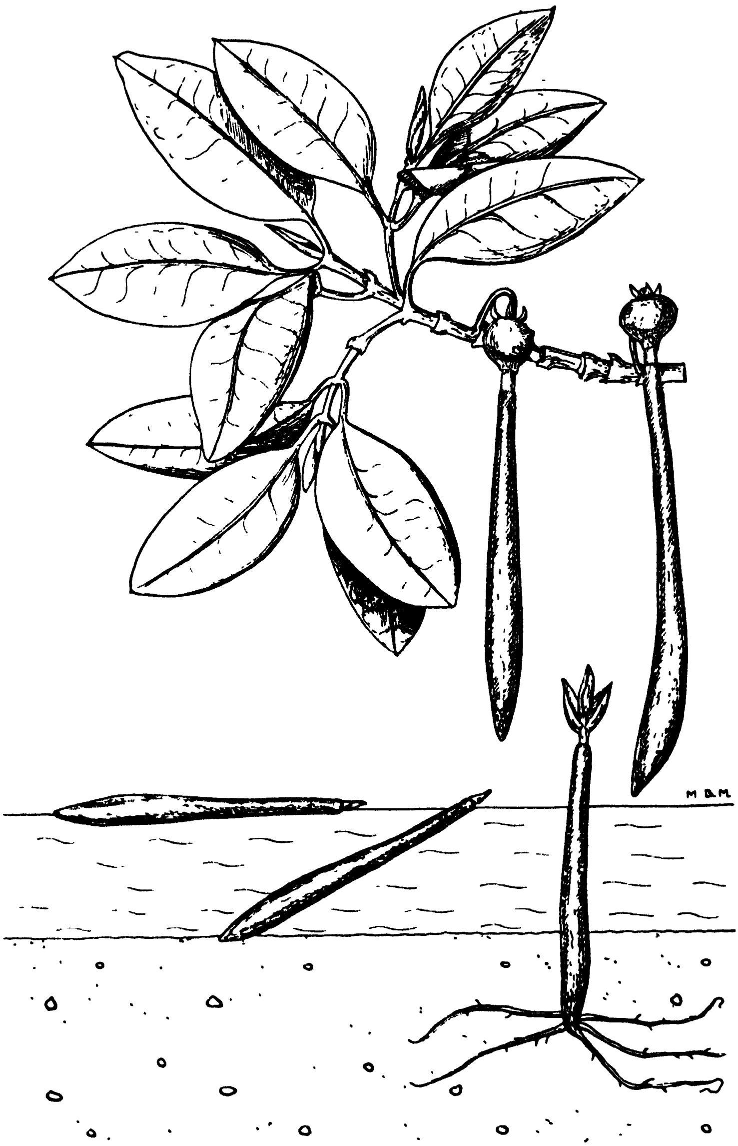
In *Rhizophora* 95 per cent. of the seedlings float. Out of 5 seedlings of R. *mucronata*, 3 were afloat and healthy after 87 days, and out of 20 seedlings of R. *mangle*, 16 floated after 90, and 4 after 120 days.

The ovary, a large brown conic or pear-shaped body in *Rhizophora*, falls with the seedling, but becomes immediately detached, and the cylindric seedling floats freely away. It now consists of the long green radicle and a small plumule.

The seedlings usually float horizontally in the sea; I have, however, sometimes seen them floating vertically. Guppy says they float vertically or steeply inclined in the fresh water of estuaries. He points out the importance of the horizontal posture of the seedling in preventing the plumule being exposed to the sun and withering, as it might if the seedling floated erect. The horizontal position has, however, another important function to fulfil. When the seedling floats to a shallow water spot where it can grow, the sharp point presses against the mud and becomes more or less embedded in it. As the tide rises, it is pushed up into a vertical position, and this pressure keeps the seedling in an erect posture, as the radicle continues to penetrate the mud, and the leaves expand.

Seedlings, if cast up on a beach, can survive for some time. Guppy planted 5, which had been found stranded on a beach and kept dry for 9 weeks, and

PLATE XIV.



DISPERSAL BY WATER.

Rhizophora conjugata (branch with fruit, floating and rooting seedlings).

[*To face p.* 288.

in 14 days, after planting in Mangrove mud, they developed their first leaves. If covered with vegetable debris and sand, they might last for many months, he says. However, I would point out that seedlings lying horizontally on a beach could not attain the erect position necessary for their development, unless they were washed off again by a rising tide and floated into a suitable spot.

The story of the other *Rhizophoraceae* is much the same as that of *Rhizophora*. There are 4 genera, *Rhizophora* (4 species), *Bruguiera* (4 species), *Ceriops* (2 species), and *Kandelia* (1 species). Of these, the last 4 genera are Asiatic, and 1 species ranging as far as Polynesia, East African, *Rhizophora* alone being found in America and West Africa, and comprising 3 or 4 species. Of these R. *mucronata* is the most widely dispersed—in Africa, at Yemen in Arabia, Abyssinia coast near Aden, Massawa, Somaliland and South Africa, Natal (most of this coast is sandy, so the plants are scattered), Mascarene Islands, Seychelles, Madagascar, Aldabra, Comoro, India (both coasts), Ceylon, Mergui, Andamans, Malay Peninsula and islands to Australia, Liukiu, Formosa, Marianne Isles, New Caledonia, Polynesia (excluding Hawaii, Tahiti, Krakatau, Cocos and Christmas Islands). R. *conjugata*.—South India, Ceylon, Siam, Cochin China, Malay Peninsula and islands to the Admiralty Isle. R. *racemosa*.—Guiana and West Africa. R. *mangle*.—South America, from Florida southwards, and Fiji and Tonga. Guppy describes an intermediate form, *Selala*, which does not fruit, apparently a hybrid between R. *mucronata* and R. *mangle*, in Fiji.

The occurrence of R. *mangle* in Tonga and Fiji has only recently been recorded. Hemsley suggests that it has lately been introduced to Tonga in ballast, but, considering the soft nature of the seedling, this seems to me quite impossible. Guppy shows very fairly that it is abundant in Fiji, and has hybridised with the Asiatic species. I think it is clear that it must have been drifted by sea to these Polynesian Islands from America, although the distance (at least 6,000 miles) seems a very long one. It may, however, have formerly established itself on some of the intermediate islands, and either been overlooked or has disappeared, from changes in these islands. Guppy does not accept the idea that it has been drifted by sea to the Fiji Islands from South America, but says: " Rather is its present distribution (to be) regarded as representing its " original range over the Tropic zone." It is difficult to see why, in that case, it should not have persisted in some other portion of the globe. As we have seen, it would not be the only case of a sea-migrant having travelled from America to Polynesia.

Bruguiera.—There are 4 species of this genus. Two of them, *B. gymnorhiza* and *B. eriopetala*, grow as trees mixed with the *Rhizophoras*. They have large flowers and sausage-shaped, cylindric, short, thick radicles, 3 to 9 inches long and about ½ of an inch thick (Pl. XIII, fig. 11). Guppy kept a seedling of *B. gymnorhiza* floating safely for 117 days. The thickness of the radicle is of advantage to these floating seedlings, as when attacked by molluscs during their travels, the thicker ones are less likely to be bitten in two, and many, only slightly bitten, survive. The plants with the stoutest radicles, *Rhizophora* and these two *Bruguieras*, are the most widely-spread species and the most abundant. It is possible that the strong tannin in all parts of the plants protect them from injury from some marine molluscs. In *B. caryophylloides* and *B. parviflora* the flowers are much smaller and the radicles long and slender. These are smaller trees, often shrubs growing along the edge of the tidal rivers and Mangrove swamps. They are less common and less widely distributed. *B. gymnorhiza* is the most widely-distributed species, ranging from East and South Africa to the Seychelles Madagascar, Aldabra, India, the Sundribuns and Travancore, Andamans, Ceylon, Malay Peninsula and Islands, Cochin China, Hongkong, Australia and Polynesia. *B. eriopetala* is more local, or perhaps, overlooked, as it resembles the last. It ranges from South India, Cochin China,

Siam, Malay Peninsula to the islands. *B. caryophylloides* ranges from Ceylon to Burma, Siam, Malay Peninsula, through the islands to New Guinea; and *B. parviflora* from Mergui, Andamans, Malay Peninsula and Islands to the Philippines.

Ceriops Candolleana is found from East Africa, Madagascar, Seychelles, Aldabra to both coasts of India, Ceylon, Siam, Malay Peninsula and islands to New Guinea, and the Philippines and New Guinea. It is not known from the Malay Peninsula. In these plants the radicles are slender and rather short.

Kandelia Rheedii is less common—India, Sundribuns and Mangalore, Malay Peninsula (rare), Borneo, Lantau Island, Hongkong, Liukiu and Formosa. Its radicles are from 9 to 15 inches long, and slender.

COMBRETACEAE.

Lumnitzera.—Of this genus there are 2 species, one shrubby with white flowers, *L. racemosa*, the other a tree with scarlet flowers, *L. coccinea.* The fruit is elliptic, or club-shaped, rounded, 1-seeded, ½ to 1 inch long, $\frac{1}{16}$ inch through, with a very small seed in the centre.

Both species cover approximately the same area, but *L. racemosa* extends the farthest. It is found in East Africa as far north as Dar-es-Salaam, and in almost all the Mascarene Islands, including Aldabra, India, Ceylon, Maldives, Andamans, Siam, Malay Peninsula and islands, Formosa, Hongkong and New Caledonia, Krakatau (1919). *L. coccinea* occurs in the Seychelles, Ceylon, Mergui, Andamans, Maldives, Malay Peninsula, all the Malay Islands (but not Cocos-Keeling, Christmas Isle or Krakatau), Formosa, New Caledonia and Polynesia. Fruits, however, were found floating off Cocos-Keeling. Guppy classes it as a Mangrove plant. I have always seen it in the sandy belt behind the Mangroves.

The buoyancy of the *Lumnitzeras* is due to the buoyant tissue of the fruits, which float for months.

Laguncularia racemosa.—This tidal-swamp tree has a small, narrow, oblong fruit, something like that of *Lumnitzera.* According to Schimper and Guppy, it is the light pericarp by which it floats. In the figure in the " Flora Braziliensis " there is a space represented between the seed and the pericarp, so that the seed does not quite fill the cavity, which may aid in floating it. The plant is chiefly South American, occurring on both coasts from Florida to Brazil, including Fernando de Noronha and the Galapagos, and also occurs in West Africa. It grows in tidal mud like a Mangrove.

Conocarpus erectus is also a tidal swamp shrub of South America from Florida to Brazil, including the Galapagos, Cozumel Island off Yucatan, and Margarita off Venezuela. It also occurs in Western Africa. The flowers are borne in a small head forming a cone-shaped infructescence of small, flattened, recurved ovate fruits, each 1-seeded, the pericarp of which (the buoyant organ) is thick in proportion to the small seed.

Quisqualis indica is a climbing shrub, often cultivated for its red flowers. The fruit resembles that of *Combretum trifoliatum*, oblong with 5 angles, corky and light. The plant, in a wild state, inhabits river banks, where the seeds are easily drifted along by the current, and I have found it wild on the banks of the Pahang River, on the east coast of the Malay Peninsula. It occurs apparently wild in Burma, Java, Wetter Island, Sulu, New Guinea and Formosa; also in Christmas Island, which it must have reached by sea. It is perhaps wild in West Africa, but doubtfully so in India, the Seychelles, and South America.

Terminalia catappa.—The Indian Almond is a large tree, common on sandy beaches by the Asiatic and Polynesian shores, where it is wild. It is, however, very often planted as a roadside or ornamental tree, and as such has an even

wider distribution. The fruit is an oval flattened drupe about 3 inches across. It floats readily in the sea for many months, its buoyancy being due to its fibrous pericarp, which lasts a considerable time in sea-water. The tree is certainly wild in Bonin, Hainan and Formosa Islands, Andamans, Diego Garcia, Malay Peninsula and islands, including Christmas and Krakatau, and Cocos-Keeling; New Caledonia, New Hebrides, Samoa, Fiji and other Polynesian islands, Madagascar, Mauritius, Seychelles. It seems quite absent as a wild plant from India, Ceylon, Africa and Hawaii, though it has been introduced into all these countries as well as Arabia, the Persian Gulf and South America, and the West Indies; but Guppy has seen fruits in the Hawaiian shore-drift, and they have apparently been drifted from cultivated plants to the Bermudas and Asseradores Island off Nicaragua, and Guppy has seen its fruits in beach-drift in Jamaica, Colon and Turk's Island.

He suggests that *Terminalia catappa* took its origin in America on account of there being a number of species there, but the genus is even better represented in tropical Asia than in South America. Furthermore, none of the American species are really allied to *T. catappa* except *T. latifolia*, of the West Indies, which certainly resembles it in fruit and foliage. In the Malay Peninsula we have several inland, usually river-bank, trees which have the remarkable oval flattened fruit of *T. catappa*, from which this species may have been derived, but most of the species in the genus, on both sides of the globe, have angled or rounded fruits, and many are winged.

MYRTACEAE.

Barringtonia.—These Asiatic shrubs or trees, with long pendent racemes of flowers and large 1-seeded fruits, fall into 3 groups as regards dispersal. A small number inhabit inland woods (*B. pauciflora*, *B. macrostachya*, *B. sumatrana*). They are oblong, fleshy green fruits, and are dispersed by squirrels or other rodents, which carry off the fallen fruit to eat the fleshy pericarp. Their area of dispersal is limited.

A second group (*B. spicata*, *B. acutangula*) are shrubs found only on river banks, with long pendent racemes hanging over the water, into which fall the comparatively small oblong fruits, which are readily drifted down stream. The species included in this group are all very closely allied. They range from India, Siam, Pulau Condor, Mergui, Burma, the Malay Peninsula and islands to Australia and Samoa. They are probably sea-dispersed to a limited extent, but seem always to be absent from remote islands.

The third group, including *B. speciosa*, *B. racemosa* and their allies, are almost exclusively sea-dispersed, and are well adapted for this purpose. I may mention, however, that I have seen fruits of *B. racemosa* in the Singapore Gardens, carried off by squirrels or rats, though practically the same kind of fruits were refused by rats and crabs in Christmas Island.

Barringtonia racemosa, in the large sense, is a shrub rather than a tree, with fleshy fruits, oblong or egg-shaped, about 3 inches long and 1 ½ inches through, green to pinkish-red in colour. The shrub usually inhabits damp spots near the sea, backwaters, lakes, etc. In Christmas Island it grew on coral detritus at the foot of the hills. In some places it is cultivated for ornament, and may thus be found inland, but it is undoubtedly mainly sea-dispersed, though it drifts up tidal rivers for a long way. It is found in East Africa (20 miles up the Zambesi River) South Africa, Madagascar, Seychelles; Madras (canal banks), and Ceylon (probably native, but planted also); Siam, Andamans and Nicobars, Malay Peninsula and islands, including the islands Siberut and Sipora (west coast of Sumatra), Amboina, Wetter Isle, Christmas Isle, Krakatau, Solomon Islands, Samoa, Fiji. In coral islands, where the soil is unsuitable, it is not

found, but fruits of 2 species of the genus have been drifted up on Cocos-Keeling Island, where, however, neither has established itself.

The fruits, which float for many months, owe their buoyancy to the thick fibrous-fleshy pericarp.

B. speciosa is a rather bigger tree than *B. racemosa*, with larger and more showy flowers, and a very large, almost square, 4-angled fruit with a broad base, 4 inches or more through, with a very thick fibrous spongy pericarp. The tree inhabits sandy spots on the seashore. Though very widely distributed, it is not so common as *B. racemosa* on account of its requirements of sandy beaches, less abundant than damp Mangrove or tidal mud in the tropics. Added to which the tendency to plant towns on such spots as it is likely to establish itself on has doubtless caused many of its original habitats to disappear. In Singapore it was scarce as a wild plant, but in one part of the town there were a number of trees adopted as roadside trees which I am convinced were the relics of an old-established native habitat.

Mr. Buckland (*Nature*, 1888, p. 421) records the drifting of a sound fruit of this plant to South Africa, but it has not established itself on that continent. It is found in Seychelles and Comoro Islands, Ceylon (on the south coast, but very rare, and not recorded by the early collector, Hermann), Andamans, Malay Peninsula and islands, including Krakatau, to the Philippines and Admiralty, Marshall Isles, Ducie Isle, New Hebrides and Polynesia. An early record of a tree with square fruit on the Cocos-Keeling Island suggests its former occurrence here. As in *B. racemosa*, the fruit, which floats for months, owes its buoyancy to the spongy fibrous pericarp.

B. Vriesii is recorded as occurring in Krakatau after the eruption. I have seen no specimen of this plant, which is said to be a native of Bantam in Java. Van Leeuwen points out it is a local inland species and the identification almost certainly erroneous. It was doubtless *B. racemosa*.

B. conoidea, a tidal swamp or tidal river-bank species, is found in Mergui, the Malay Peninsula, and Borneo. This has not a very wide distribution, but I believe it owes its dispersal to water.

LYTHRACEAE.

Pemphis acidula is a low bush or small tree, growing usually on coral reefs in the splash of the sea. The fruit is a very small capsule containing a number of small seeds with the spongy testa drawn out into a wing. The buoyant tissue of the seeds lies in the testa ; they float for months. The plant is widely distributed from East Africa at Dar Es Salaam, Madagascar and most of the Mascarene Islands, including Aldabra, on the coasts of India and Ceylon, the Andamans, Mergui, and Pulau Condor and Koh Pennam, off the Siamese coast ; very rare in the Malay Peninsula, and confined to one spot in Singapore, Java, Christmas Island, Cocos-Keeling, Celebes, Timor, Timor Laut, New Guinea, Australia, New Caledonia, Polynesia and Formosa (on sandy cliffs).

It is a regular coral-reef plant, and, like *Tournefortia argentea*, a plant of similar habit, is only to be found in one spot in the Malay Peninsula. The west coasts of the Malay Peninsula have shores of tidal mud only, and those of the east coast are mainly sandy beaches. There is no elevated coral beach, and the soil of the Peninsula is very deficient in lime. The plant has not settled yet at Krakatau (1919), perhaps for some such reason.

Sonneratia.—Usually big trees growing in sea mud or tidal rivers. The fruit is round, fleshy, surrounded below by the stiff calyx lobes, the seeds small and angular. There are about 4 species, which have been somewhat confused, as they make rather poor herbarium specimens, and are not so well collected as they should be. Except that one species gets to East Africa and the

Mascarene Islands and Australia, they are confined to the shallow seas or tidal rivers of tropical Asia.

S. acida, with pink stamens and petals, is chiefly a tidal estuary plant in India (both coasts), Ceylon, Burma, Malay Peninsula, Siam, Java and Timor. It occurs in the Maldives, but is said to have been introduced there.

S. alba ranges from Mombasa (East Africa), Madagascar, Aldabra, Seychelles, Malay Peninsula and the larger Malay Islands, to New Caledonia and Australia. *S. apetala*—India, Ceylon, Burma; and *S. Griffithii*, India, Burma, Andamans, Malay Peninsula and Borneo. *S. alba* and *S. Griffithii* grow usually in shallow tidal mud seas, so that the water is almost always over the roots. It is not to be wondered at, therefore, that they are absent from the smaller islands and coral atolls. The seeds owe their buoyancy to the light testa. The fruit gets soft and breaks up in the sea, releasing the seeds.

FICOIDEAE.

Sesuvium Portulacastrum.—There is some difficulty about this species, as I find in books and herbaria very different-looking plants combined under the same name. Some are apparently inland plants with small or large spathulate leaves. The common seashore form or species has fleshy linear leaves and rose-pink flowers. It is a herb with subsessile axillary capsules containing numerous small, round, black, polished seeds, and usually grows among rocks on mud, or on muddy spots on the shore, never inland (in sand, according to Trimen, in Ceylon), and is a native of Bengal, Madras, Andamans, Maldives, Minikoi, Siam, Malay Peninsula and islands, including Christmas Island and Cocos-Keeling Island, Australia and Polynesia, Phoenix, Cook Isle, Maldon to Hawaii, Formosa, Canton, Liukiu, America from Florida southwards, Bermudas, Galapagos, Rodriguez, Aldabra, West Africa.

In Fernando de Noronha there was an endemic yellow-flowered species, *S. distylum* Ridl., much after the same style.

This fleshy herb is undoubtedly dispersed by sea, both by its seeds and by portions of the plant, but it was also dispersed to some extent by the boobies in Christmas Island, which used bits of the plant in making their nests. According to Guppy, the seeds have no buoyancy and sink very speedily. If this is always the case, the plant must be distributed simply by broken-off fragments, either drifting in the sea or carried by sea-birds, but I have seen it in spots where sea-birds were quite absent at the present day. I suppose it to have been of American origin, as there are a number of species and forms there. It evidently has spread about the coasts very readily, though it did not appear at Krakatau till 1919.

CUCURBITACEAE.

Luffa cylindrica.—(*L. insularum*).—This Gourd seems to be truly wild in Polynesia and the eastern Malay Islands. The form known as *L. insularum* is apparently a maritime form of the typical *L. cylindrica*. Though often cultivated, it was found by Banks and Solander in Tahiti when that island was discovered, and so, doubtless, is wild there. The fruits are long and cylindric, and become dry and skeletonised. The apical disc falls off, and the flat round seeds fall out through the hole at the tip. Some, however, remain entangled in the fibrous skeleton. Guppy has seen the fruits floating down the Rewa River in Fiji, but found they did not float for more than a week in fresh or salt water. The seeds will float for months. Out of 100 seeds, 60 floated for more than 2 months. The buoyancy is caused by the unfilled space in the seed cavity. The cultivated form, he says, has non-buoyant seeds. It occurs in Australia and in Malay Islands as well as in Fiji, Tahiti, New Caledonia, Tonga, etc.,

and was found in Krakatau in 1919. I have never seen any species of *Luffa* wild in Asia, but several are commonly cultivated.

Fruits of some other *Cucurbitaceae* have been found drifted up on the coasts of Norway, and these are generally referred to as *Lagenaria vulgaris*, the Bottle Gourd. Sernander states that they were generally worked Calabashes, but records one containing seeds. They were found early, and are noted in the Norway beach-drift in the 18th century. There is some doubt, however, whether some of these were not fruits of *Crescentia* (*Bignoniaceae*).

Fevillea cordifolia, a large Pumpkin growing on river banks in South America and the West Indies, is dispersed by falling into the river, after which it decays, and the seeds (about 10 in number), which are flat, round and 2 inches across, float away, but Guppy shows that though they reach the sea from the river, the seeds are all or almost all decayed. It is possible that some might drift along the coasts and be carried up rivers near by in a living state. In one case he kept a seed floating for 2 months in good condition, but in most the kernel decayed before that.

Similar to this case is that of *Hodgsonia capniocarpa*, of the Malay Peninsula and Borneo, the gourd of which floats down the rivers and the dead seeds are picked up on far-distant coasts. I have found them in Cocos-Keeling Island. These are river-dispersed plants, but not sea-dispersed.

UMBELLIFERAE.

Crithmum maritimum (Samphire), a seashore rock plant, common on our coasts, and also found along the Mediterranean shores as far as Palestine, also in Madeira and the Canaries.

The fruit separates into the 2 mericarps, which float readily in sea-water for a year or so. In Guppy's experiments 95 per cent. floated for 10 months. He notes that in sea-water the spongy coat of the mericarp retains its vitality, but decays in fresh water, when they cease to float, so that they float only for weeks in fresh water, while they float for months in the sea. They are light enough to be blown high up the cliff-face in the spray in a moderate gale. Indeed, one usually sees the plant high up the cliffs near the sea, where the carpels have been blown up by the wind. The walls of the mericarp are of a spongy cellular air-bearing tissue.

Apium graveolens.—The fruits of the Celery are stated not to float at all. The plant in a wild state is an inhabitant of river banks, inland and tidal. The species occurs all over Europe to Afghanistan, India, Korea, Mexico, Peru, Ecuador, Falkland Islands and the islands of Azores, Madeira, Hainan, Elizabeth Island (Magellan).

How far exactly this distribution is due to cultivation and accidental introduction by man is not certain, but it is known to have been carried about and planted with other vegetables by the very early voyagers.

A. australe.—As far as is known to me, this plant has never been cultivated, and the fruits are believed to sink in water. It is very largely an island plant of the Antarctic region, and is found in Brazil, Paraguay and the Falklands, Lord Howe's Isle, Kent Group, Glenny Isles, Australia, Tasmania, New Zealand, Tristan d'Acunha, Inaccessible Island, Gough Island, Moncoeur Island (Bass Straits) Kermadec, Lifu and South Africa.

The mericarps of the small fruit have 5 rounded, projecting, corky inflated lobes, and can doubtless float. Its inland distribution makes it very probable that it is sea-disseminated, but it may also be transported on birds' feet in mud.

Ligusticum (*Haloscias*) *scoticum.*—The Lovage grows on rocks and beaches in the north temperate region, from Arctic or sub-Arctic Europe to Kamschatka and Japan, and in Arctic America. The mericarps float for 2½ months,

according to Praeger. They are rather elongate, with six prominent ridges, but they are not thick and corky as in the Samphire, though the plant is much more widely distributed. This is probably due to its arctic habit, there being a longer area of sea by which it could travel round the northern region. I find it recorded from the Faroe Islands, and on a rocky islet in the Estuary of Fleet, in Kirkcudbright, to where it was, no doubt, drifted by sea.

Eryngium maritimum.—The Sea Holly, though a sea-sand dune plant of wide distribution in Europe, seems to possess poor floating powers. Praeger says the fruits float from 2 to 4 days, and all sink in a week. It appears to be absent from islands like the Canaries and Azores. The fruits can be blown along the land, and Guppy thinks it may be carried by its sharp spines attached to the feathers of birds. I am doubtful as to its methods of diffusion.

RUBIACEAE.

Morinda citrifolia.—Of this genus of trees and climbers there are a number of species described somewhat confusedly, as herbarium specimens are often not very good. The one most certainly sea-dispersed is a small tree about 8 or more feet tall, with large, rather fleshy leaves and a head of fruits about 3 inches long and 2 inches through, oblong and fleshy, juicy translucent white. It is composed of a large number of ovaries connate in a mass, each containing 4 small brown pyrenes. This is, I believe, the true plant known as *M. citrifolia.* The fruit is occasionally eaten, but is rather nauseous and not popular. The roots supply an orange-red dye which is valued by natives, and mainly for this reason the plant has been carried about and cultivated. The woody pyrenes, about ¼ of an inch long, contain an air-space, the small seed not filling up the whole pyrene. Some other species are reported to have this flotation structure, e.g., *M. angustifolia*, of India, but in most species the seed fills up the pyrene. Schimper compares the pyrenes of *M. citrifolia* with those of *M. umbellata*, which, as he shows, have no air-space. This latter plant is a scrambling shrub usually abundant on Asiatic sea-coasts, and widely spread, but the fruit-heads are small, 1 inch or so through, conspicuously orange-coloured, and undoubtedly bird-dispersed. Some of the other inland species, such as *M. elliptica*, have small, green, inconspicuous heads of fruit. This latter tree inhabits the open country inland, cliffs, and banks by the sea, and is one of the first woody plants to appear in the fields of Lalang Grass (*Imperata cylindrica*), which replace the forests of Malaya after they have been burnt. The fruits of this are, I believe, chiefly dispersed by small fruit-bats, possibly also by birds. It has long been confused in herbaria with *M. citrifolia*, but in life the two plants are utterly dissimilar.

M. citrifolia is found on both coasts of India, and in Ceylon, but is doubtfully indigenous there. It occurs also in the Andamans, in Diego Garcia (Chagos), in Siam, Sumatra, Java, Cocos-Keeling Island, Borneo, on Krakatau, the Philippines and Polynesia. In the Seychelles it is probably an introduced plant, as it certainly is in San Domingo, St. Vincent and Guadeloupe. It is not uncommon in gardens, village compounds, etc., in the Malay Peninsula, but certainly not wild there. It may have reached Cocos-Keeling by sea, as, if it is rightly identified, it has done to Krakatau, but I know that Ross, of Cocos Island, had at one time an idea of planting it on a large scale, for the dye obtained from its roots. The plant appears to have originated in Polynesia, as it is abundant there, but it has been widely diffused in cultivation as a dye-plant, and it is difficult now to say where it is indigenous. It is possible that it is altogether a cultivated plant, derived from *M. bracteata* or some such plant,

but it seems to have spread of itself, widely by sea in the Malayan and Polynesian Islands.

Guppy says that the fruit falling into the sea decays and the pyrenes drift away and can float for 53 days. It is also almost certainly disseminated by birds and bats (Pl. XIII, figs. 6 and 7).

M. bracteata is an allied species at least, if not the ancestor of, *M. citrifolia*. It has similar fruits, 1 inch long, in which the pyrenes possess an ovoid empty cell, according to Roxburgh, as has also *M. multiflora*. Both species are Indian, and the former is widely distributed about the Malay region, but has been confused much with *M. citrifolia* by botanists. It is this plant which I believe I found on rocky places about the sea in Christmas Island, and have found it also in the Malay Peninsula in similar localities. It is found also in Amboina, Celebes, Timor Laut and other Malayan Islands.

M. Royoc is a New World species which grows on the sea-coasts of the West India Islands, including the Bermudas, as well as Florida, Honduras and Panama. The plant has more of the habit of *M. umbellata* than of *M. citrifolia* or *M. bracteata*, as it seems to be often a climber. The heads of fruit are as large as a walnut, and the pyrenes have the same structure as those of *M. citrifolia*, and float for at least 5 weeks (Guppy).

Scyphiphora hydrophyllacea, a low shrub or bush about 4 feet tall, with small white flowers and green drupaceous fruits containing 2 corky, woody pyrenes about $\frac{2}{5}$ inch long, with 4 or 5 rounded longitudinal ribs. It frequents muddy shores in tropical southern Asia, and its pyrenes are to be seen in very large quantities along the coast of Malaya. It ranges from Madras, Ceylon, Andamans, Tonkin and Siam, the Malay Peninsula, and almost all the larger Malay islands to North Australia and New Caledonia. It has not, however, reached the African region, and is absent from Bengal and from Polynesia, as well as from Krakatau and Christmas and Cocos-Keeling Island. It is probable that its absence from these localities is to some extent due to their soil-unsuitability, but I have no record of the pyrenes having been found in sea-drift of any of the areas where the plant is missing.

Guettarda speciosa.—The genus *Guettarda* is very well represented in tropical America, but is hardly represented at all by any species in the Old World, except by *G. speciosa*, a tree occurring on all coasts and islands from East Africa to Polynesia. The tree is low, but large and much-branched, and bears round or ovoid, depressed green fruits about $\frac{3}{4}$ inch through, with a woody stone, from 4- to 9-celled.

The genus is closely allied to *Timonius*, in which the fruit consists of from 12 to 30 small, 1-seeded pyrenes, which cohere by their sides and form a stone-like body. In these trees and shrubs the fruit is dispersed by birds, which eat them, except one species, *T. Finlaysonianus*, a tidal-mud shrub on the coasts of the Malay Peninsula and Sumatra, which appears to be dispersed by tidal rivers.

The seed or stone of *Guettarda* floats readily, from its strong cork-like, hard outer coat, and it can drift for very long periods, for as much as 50 days (according to Guppy), in the sea—many months at least. I have, however, found it sunk in the sea on the shores of Christmas Island. The tree usually grows in sandy or gravelly beaches, and is found in East Africa, Pemba, Zanzibar, Galiga Isle; Seychelles, Aldabra, Comoro, Madagascar, Amirante, Diego Garcia (Chagos); Andamans, Ceylon, Siam, Cochin China, Pratas Island off China (where it forms the bulk of the vegetation); Malay Peninsula and islands, including Christmas Isle, Cocos-Keeling and Krakatau, North Australia and Polynesia. It is absent from Peninsular India and West Africa, South America and Hawaii. There was an endemic species, *G. Leai*, in Fernando de Noronha, but it was an inland species with small fruits, and, I suppose,

was introduced from the mainland by birds; and there are several species in Hawaii and Fiji which are probably bird-introduced, and of which the fruits float for a few weeks only and soon decay. One inland plant, *Guettarda speciosa* var. *tahitensis* of Tahiti, however, seems to be a derivative from the littoral plant.

From the distribution of the genus it seems likely that *Guettarda* originated in South America, and one species adapted for sea-dispersal migrated to Asia through Polynesia.

COMPOSITAE.

Wedelia biflora.—A common herbaceous yellow-flowered Composite on the muddy and sandy shores of the Old World tropics. The achenes are unprovided with a pappus. They are triquetrous hairy cuneate, oblong, thick and corky. The plant ranges from East Africa, Pemba, Zanzibar, Madras, Ceylon, Andamans, Laccadives, Minikoi, Siam, Malay Peninsula and islands, including Christmas Isle, Cocos and Krakatau, Timor Laut, Australia, Norfolk Isle, Cook Isles and Polynesia, Formosa and Hongkong. The seashore creeping *Wedelia* (*W. prostrata*), of China and Japan, is probably an evolution of this plant. It appears to grow in sand dunes. I found an odd form, shrubby, with small leaves and flower-heads, not very unlike it, growing in sand-hills in the Adang group of islands in the north of the Peninsula.

Penzig gives 3 species as occurring in Krakatau, *W. asperrima*, *W. glabrata* (both forms of *W. biflora*), and *W. scabriuscula*, and *Wollastonia* sp. I have not seen any of the specimens, but *W. glabrata* is apparently a form of *W. biflora*, and *Wollastonia* is synonymous with *Wedelia*. *W. asperrima* is an inland plant much resembling *W. biflora*, but the achenes are not so thick and corky. I suspect the identification is doubtful.

Matricaria maritima.—This appears to be a form of the now very widely spread *M. inodora*, which frequents sea-coasts. The fruits (achenes) of *M. inodora* have no floating powers, but those of *M. maritima* float for as long as 8 months. Praeger gives the achenes of *M. inodora* as floating for 12 hours only. The fruits in both are oblong, with the pappus reduced to a crown, and 3 projecting ribs run down the body of the achene, which is otherwise smooth. In *M. inodora* these ribs are comparatively low in comparison with the body of the achene; in *M. maritima* they are much thicker and more corky, and the body of the achene is much smaller in proportion. *M. inodora* is, in England at least, an annual weed of cultivation. It is not recorded in this country by Reid as appearing till neolithic days. *M. maritima* is a perennial Arctic plant found on seashores as far south as Northern Spain. It seems to be abundant in Norway, Iceland, Spitzbergen, Faroes and Nova Zembla and Northern Siberia. The achenes are spread by currents in Arctic Norway, and are found in beach-drift. They have a layer of buoyant tissue beneath the epidermis, the corky ribs and pericarp much as in *Wedelia*.

Ambrosia crithmifolia (*A. hispida*), a small sand-beach herb with little dry achenes enclosed in a persistent involucre, is (according to Guppy) abundant in the West Indies and the Keys of Florida, but is absent from the Bermudas. The fruits in the involucre occur in abundance on the beaches, and could easily be swept off by the waves. They sink in 2 to 4 days. Lansing observes that they are one of the earliest plants to occupy land newly gained by accretion from the waves. No doubt the fruits could be driven along the sand-banks by wind, and also float for some distance in 2 to 4 days. As Guppy suggests, they might be washed into the crevices of timber, temporarily stranded. In shallow seas they might be washed along the bottom and thrown up with the sand, and possibly whole plants or fruiting branches might float. *A. maritima* occurs in Europe, Africa and South America, but is scarce in the latter. The

fruit is very hairy and the pericarp thick. It forms bushes along the edges of the Nile. It is probably disseminated by water to some extent, but is really more of a sandy-desert plant than a littoral one.

Launea pinnatifida, a creeping seashore plant, with plumed achenes. Willis and Gardiner (in " The Plants of the Maldives ") class this as a plant dispersed by sea-currents. They say it is one of the first plants to appear on a bare sand-bank, and the outermost plant on a growing sandy beach. It occurs in Egypt, East Africa, Mauritius, Aldabra, Assumption Island, India, Ceylon, Laccadives, Maldives, Minikoi, Andamans, Burma, Cochin China and Hongkong. It appears to be quite absent from the Malay region. It is easy to understand these plumed achenes of this plant drifting along sandy coasts, but it is less easy to see how it has gone to the islands unless by sea-drift. It is possible it has reached them by wind, but the distances are rather extensive. The achenes, however, are cylindrical, oblong, $\frac{1}{8}$ inch long, and the outside appears corky; the plume is very readily detached. The outer coat, i.e., the calyx-tube, appears thick in comparison with the seed, and it might readily float. In a plant like this, however, one must always take into account the possibility of the transport of its achenes in ballast to some at least of its localities. Its absence from Malaya is rather striking.

GOODENOVIACEAE.

Scaevola.—The headquarters of this genus appear to be Australia and Polynesia, from which some species range westwards through the Eastern Malay Islands; they are shrubs with drupaceous fruits. Two of them, however, are adapted for sea-dispersal, and go much further. *S. Koenigii* is a herbaceous seashore shrub with fleshy leaves and white drupaceous fruit, and grows abundantly in sandy spots along the east Asiatic coast. It is possibly to some extent bird-dispersed, but mainly travels by sea. It is found on most Polynesian Islands, North Australia, Liukiu and Bonin Island, Pratas Island off Hongkong, and Formosa, most of the Malay Islands from New Guinea westwards, including Timor Laut, Cocos-Keeling, Christmas Isle and Krakatau, Malay Peninsula, Siam, Ceylon, Madras, Bombay, Andamans, Diego Garcia (Chagos), Minikoi, Laccadives, Madagascar, Aldabra, Seychelles, Mauritius, Amirante, East Africa, Pemba.

In Christmas Island it grew rather high up on the cliffs, but the sea there breaks very high in storms, and doubtless the seeds were thrown up in a gale. The coastline is mostly unsuited for it, being rocky and shingly. In Krakatau it was one of the first plants to arrive and establish itself. Its abundance in small islands and its early appearance in Krakatau seem to show it is more dispersed by sea than by birds.

The fruit of *Scaevola Koenigii* is oval-globose, about $\frac{1}{4}$ inch through, with a rather thin, white pulpy exocarp, which soon dries or decays off when the fruit falls. The fruit is thin-ribbed and dry, the mesocarp thick and corky, with 1 or 2 small seeds. They lie about dry, abundantly, under the bushes, and can readily be blown down the sand-banks into the sea. They float for 50 days (according to Guppy).

S. Plumieri (*S. Lobelia*) is more shrubby, with smaller leaves and purple or black berries. It grows in sand dunes chiefly, and ranges from Ceylon, Madras, Bombay, Scinde, Madagascar, Cape, East and West Africa to Florida, Mexico, Clarion Isle, Bermudas, West Indies, Holbox and Mugeres Island (British Honduras), Brazil and Galapagos.

The distribution of these two species is curious. They are very distinct, and overlap only in Madagascar, East Africa, and some parts of India and Ceylon. *S. Plumieri* seems to have originated in Western Africa, and gone east for a

short way, and west also to America. There is no other species in America. It does not seem to be typically an island plant, but rather a coastline one.

The genus is a large one, and there are a number of species which bear very little resemblance to either of the littoral species. The ones most resembling them are *S. montana* and *S. glabra*, of Polynesia, from which region I believe the littoral ones originated.

PLUMBAGINEAE.

Aegialitis annulata, a woody shrub with broad, round leaves, and spikes of small flowers followed by a slender linear, cylindrical, 1-seeded fruit about 2 inches long. It occurs in Mangrove swamps in Bengal, Mergui, New Guinea, Aru Islands, North Australia, Howick's Group. This plant has a very odd distribution, as it has not been found apparently anywhere between the Australo-Papuan region and the Indo-Burmese region (its records in Malacca, in some works, seem to be an error, some specimens of Griffiths', who collected it in Mergui, having been accidentally labelled Malacca). It is only conceivable that it must have formerly occurred in the intermediate Malayan region and disappeared. It does not seem to be clearly related to any living plant, and is probably an ancient dying form.

MYRSINEAE.

Aegiceras majus, a shrub which is not rare in Mangrove swamps and tidal rivers. It has long, curved cylindric fruits about ½ inch long, like horns. The single seed germinates in the rather thin pericarp and then floats about in the sea. It is found in Scinde, Bombay, Madras, Sundribuns, Ceylon, Tonkin, Malay Peninsula and the islands as far as New Guinea, Australia and the Solomon Isles, also Hongkong, Hainan and Amoy. It is absent from islands where conditions do not suit it, but I saw dead seedlings floating off Christmas Island.

APOCYNACEAE.

Cerbera.—Medium-sized trees or large shrubs growing in tidal mud or Mangrove swamps, or in sandy spots, not on sand dunes. The fruit is large and sub-globose, solitary or twin, 4 inches long, 2 or 3 inches through, smooth, green, flushed with red outside. Beneath an outer soft layer the fruit is large, oblong, with a very thick fibrous network covering, containing 1, rarely 2, comparatively small seeds. When the drupe falls into the water, the pulpy portion quickly decays, and the large fibrous stones float for many months in the sea, where all through the tropical Asiatic seas they can be seen in abundance, floating, or stranded on the beaches. There are about 5 species, 2 of which are specially common and conspicuous—

C. odollam, a tree about 20 feet tall in somewhat sandy mud, with short-tubed white flowers with a yellow eye, and *C. lactaria*, more shrubby, inhabiting tidal mud, with long-tubed flowers with a red eye. *C. odollam* ranges from Madagascar and the Seychelles to India (both coasts), Ceylon, Andamans, Siam, Hainan, Hongkong, Formosa, Malay Peninsula and islands, including Krakatau, Christmas Island (one tree, which has now disappeared, but fruits are still found on the beach), Cocos-Keeling (fruits drifted up), Australia, Cook Isles, Pitcairn. *C. lactaria.*—Siam, Malay Peninsula and islands, Admiralty, Fiji and Polynesia generally, and Australia. Light and durable as these fruits are, they have failed to establish themselves on the coasts of Africa, nor have they drifted to America.

Ochrosia is a genus of trees similar to *Cerbera*, but with smaller flowers and fruits. A few inland species have fruits small enough to be transported by birds.

O. borbonica has a fruit 2½ inches long and 1 ⅞ inch wide, with a hard woody endocarp. It is found in Seychelles, Mauritius, Ceylon, Andamans, Adang Islands off the Malay Peninsula, Java, Sumatra, Borneo, Amboina, Cocos-Keeling, Philippines, Bonin, Shortland Isle (Solomons).

O. ackeringae is found in Bangka, Pulau Siberut off South Sumatra, Java and Christmas Isle. The fruit of this is yellow, and only 1½ inches long and ⅞ inch through. The Christmas Island form is remarkable for its very narrow leaves. The fruit is not too big to be carried by birds such as pigeons, but it is probably sea-borne.

O. parviflora grows in Java, Sumatra and the Philippines, Fiji, and Cocos-Keeling. The fruits are much bigger than those of *O. borbonica*, nearly 3 inches wide, and, when deprived of the outer fleshy coat, is covered with a network of fibres like that of *Cerbera*. There are a few other inland species in which the fruits are usually smaller and bright-coloured, evidently bird-dispersed.

Ervatamia (*Tabernaemontana*) sp.—Moseley found fruits and seeds of a species allied to, or identical with, *E. aurantiaca*, of Rawak, washed up in great abundance on the shores of the Admiralty Isles, Aru Island and New Guinea. The fruit is bright red and the pericarp readily destroyed by the sea. The seeds, which have a rugose corky testa, were drifted about in the sea. Most of the seeds of this group of plants have a red aril, and are dispersed by birds.

ASCLEPIADACEAE.

Sarcolobus and *Finlaysonia*.—In the large order of *Asclepiadaceae* the fruit consists of a capsule or pair of capsules, dehiscing on one side and discharging a large number of plumed seeds, which float away on the wind. There are, however, some exceptions in the form of 3, or perhaps more tidal-mud plants, in which the plume is quite missing, and the seeds dispersed by water. These are *Sarcolobus globosus* and *S. carinatus*, and *Finlaysonia obovata*, all inhabitants of the mud of tidal rivers in tropical Asia. The capsules are thick and fleshy, and the seeds flat, obovate, thin, with a thin corky margin. In *Sarcolobus* they are quite glabrous, in *Finlaysonia* they are finely hairy. The hairs, which are very inconspicuous, are rather longer at the top of the seed, as if they were the remains of a lost plume. The plants inhabit tidal mud, where they creep along, throwing up flowering stems which climb on the bushes in the mud.

Sarcolobus globosus is found in the Sundribuns near Calcutta, Mergui Archipelago, Burma, Andamans and Nicobars, Malay Peninsula and Sumatra on the island of Siberut. *S. carinatus*, with smaller seed, occurs in the Andamans and the Sundribuns; *Finlaysonia obovata* in the mouth of the Ganges, Irrawaddy and other rivers in Burma, Mergui and the Malay Peninsula.

These plants are an interesting instance of evolution for the purpose of sea-dispersal. The increased fleshiness and thickness of the capsule-walls serve to protect the unripe seed from injury due to the rise of tide. The seeds are light, with a thin corky wing, and the plume (useless to a floating seed) has disappeared. The area occupied by these plants is limited, as has been not infrequently the case in estuarine plants, on account, probably, of the carcity of estuarine rivers which the fruits might ascend with a rising tide in that region, and the seeds are too thin to endure a long sea voyage.

BORAGINEAE.

Cordia subcordata.—A stout hardwood tree with orange flowers and a round hard fruit about 1 inch through, ovoid acute, containing a single seed. It inhabits sandy seashores or coral rocks, and is mainly an island plant. It ranges from East Africa, Zanzibar, Kenya coasts to Madagascar, Seychelles, Comoro, Aldabra, Diego Garcia, Ceylon, Andamans, Mergui, Siam, Pulau

Adang, Penang and Pangkor Islands off the Malay Peninsula, Borneo, Buru, Cocos-Keeling and Christmas Island, Timor Laut, New Guinea, Australia, Cook Island, Caroline Isles, Fiji, Samoa, Tonga and most of the Polynesia islands. It is generally absent from mainlands such as India and Burma and the Malay Peninsula.

The fruits have a dense, hard but light pericarp which is light enough to be buoyant. Guppy records their floating for 40 days, and says also that they float over a year. He says that in Hawaii the trees are nearly exterminated by a moth. This may account for its absence in some localities, though it is seldom that a plant is entirely exterminated in any given locality by an insect. Where a plant is extremely abundant in close contact it may be largely destroyed, but as the plant gets scarce, so does the insect, and a recovery takes place.

Tournefortia argentea, a shrub or tree very characteristic of coral islands, and, like *Cordia subcordata*, usually quite absent from continents. The flowers are small and borne on large scorpoid cymes, and the fruit is a dry round berry about $\frac{1}{8}$ inch through. It has 4 small corky-pithy pyrenes, each containing a very small seed. The thick walls of the pyrenes are composed of fibres and cork-like cells, and are extremely light. The pericarp which holds them together is very thin and dry when the fruit is ripe. They float 40 days (Guppy). The tree grows in sandy places by the sea or on coral rocks. I have seen in Christmas Island a big tree growing on the top of a large detached block of coral. It is found in East Africa, Mozambique and in Madagascar, Seychelles, Aldabra, and most of the Mascarene Islands, Ceylon, Andamans and Nicobars, Mergui, Pulau Adang, off the Malay Peninsula coast, and Java, Borneo, Amboina, Cocos-Keeling and Christmas Island, Krakatau (one of the first plants to appear), Philippines, Aru, Admiralty, New Guinea, Australia, Bonin Isles, Pratas Island, Hongkong, Formosa and most of the Polynesian islands.

The genus *Tournefortia* is a large one, occurring in all the tropics, but, except this species, all have baccate fruit, probably bird-dispersed, though the fruits are usually green and inconspicuous. *T. gnaphalodes* resembles *T. argentea* in many respects, but the fruits are rather larger. It takes the place of the latter in the New World on the east coast of South America and the West Indies. Guppy's seeds, brought to England 12 months after being collected, all floated 6 months in sea-water and all remained sound, and several germinated 2 months later. He points out that about half of the fruits collected were seedless, and that many fall under the bushes and germinate unsuccessfully there, so that a large proportion of the fallen fruits washed into the sea may be ineffective for dispersal. This, however, is what constantly happens in seeds dispersed in any way: a very large proportion usually are wasted by insufficient fertilisation, by falling in the wrong spot out of reach of water, and being drifted, blown, or carried to an unsuitable locality.

T. gnaphalodes is (like *T. argentea*) more of an island than a mainland plant. In the view of the occurrence of tidal mud-plants on both sides of the Atlantic, Africa and America, the failure of *T. gnaphalodes* to reach Africa seems to me very significant. The sea transport of the tidal-mud plants with the land arrangement of the present day is doubtful, as stated elsewhere, but if currents could convey seeds well adapted for this from America to Africa, why is this plant absent?

Mertensia maritima.—This beautiful plant grows on seashores in the north temperate and Arctic zone. The nucules are conic, with a rather thick pericarp. C. H. Osterfeld states that they can be transported by sea-water. It is found in Iceland, Faroes, Norway, Scotland and Ireland, Manchuria, Japan, Behring Straits, Aleutian Islands and Arctic America, Greenland, Labrador, etc. It seems to be very frequent on islands throughout the regions. It is much the most widely distributed of any species in the genus.

CONVOLVULACEAE.

A considerable number of species of Bindweeds—*Ipomoea*, *Calonyction*, *Calystegia*, etc.—are undoubtedly widely sea-dispersed. Some, *Ipomoea biloba*, *I. carnosa*, *I. denticulata*, *Calystegia soldanella*, trail in sands by the seashore, and are never found inland unless temporarily, the seeds being carried in sea-sand. Their long creeping stems permit of them spreading widely over sea-beaches and allow of their carrying the seeds to a considerable distance on the far-extended shores. The stems of *I. biloba* run for 30 feet or more. The stems of the other species mentioned are shorter, usually only 2 or 3 feet long, so that the plants evolved from single seeds are not so prolific.

Some species, however, while being frequently dispersed by sea, travel for some way inland. These are climbers on rocks by the sea and on bushes and trees inland. Such are *Ipomoea campanulata*, *Calonyction bona-nox*, *Merremia nympheaeifolia*. The latter, a very large climber, was only to be found in Christmas Island on the highest part of the island, far into the interior.

It is easy to see how these powerful climbers, starting from the seashores, first scrambling over the rocks, then dropping their seeds further and further inland, and gradually progressing in the same direction, in lapse of time reach the inland forest, where they attain their full size.

Many of the other species of this order are very widely distributed over the world, and are even found on distant islands, but do not, as a rule, occur on the seashore or in such positions that they can be sea-dispersed, though some, e.g., *Ipomoea dissecta*, do grow on sandy spots not far from the sea, and also inland. Some species are undoubtedly carried about by man for the beauty of their flowers, as *Quamoclit*, *Calonyction bona-nox*, and *Ipomoea Nil*, and this may have been going on for very many years.

Ipomoea insularis, of the New Hebrides, Tonga and Hawaii, was there when the islands were first explored, but the plant appears to be, as Seeman suggests, a form of *I. nil*. Some species are apparently accidentally carried by man in soil, grain, ballast, etc. *Convolvulus parviflorus* is a very widely spread little plant. Dubiously wild in Madagascar, and Comoro, it is common in India, Ceylon, Siam, Malay Peninsula and many of the Malay islands, and it also occurs in Hongkong, Formosa, Narcondam, Little Coco, Maldives, Minikoi, New Guinea, Isle of Pines, Christmas Island (1897) on the seashore. It is generally an inland plant, I have no direct evidence of its being sea-borne, but its distribution is certainly suspicious.

Jacquemontia is an American genus of which one species is found in Hawaii (*J. sandwicensis*), an endemic, and of which I found an endemic species in Fernando de Noronha. Guppy states that the small seeds of the Hawaiian plant sink in water, and suggests that the original parent of this plant came by its seed being attached to a drifting log, and that those of the Fernando de Noronha plant (which grew near the sea, but only on the southern side and high up above the sea) came in the same way. He shows, however, in many cases of buoyant-seeded plants, that while the seeds of those of the littoral region float, the seeds of the plants growing inland do not. Is it not possible that the original ancestor of the Hawaiian plant had buoyant seeds, and that the descendant of it has now non-buoyant seed?

In the seed of *Convolvulaceae* the buoyancy is due to an unoccupied space in the testa. As a rule the embryo fills the testa more or less incompletely, and it is on the relative size of the unoccupied space that the sinking or floating depends (Guppy). In *Ipomoea biloba* and *Calonyction grandiflorum* the space in the testa is large, in *C. bona-nox*, *Operculina turpethum*, *Merremia*, and *Stictocardia tiliaefolia*, all sea-dispersed plants, the filling of the testa is irregular. Some seeds float, others do not.

It is noticeable that the 2 species with all-buoyant seed, *I. biloba* (*I. pes-caprae*) and *Calonyction grandiflorum*, are the 2 widest and most abundant species of sea-borne *Convolvulaceae*. In the others the area of distribution is much smaller (*C. bona-nox*, it is true, has a very wide distribution, but it owes much of that to man's intervention).

Here we may notice also that a structurally small difference in the seed, that mere difference in the proportionate size of the kernel (embryo) of the seed to its testa, makes the whole difference to the area occupied in the world by the plant.

I will now contrast the 2 species *I. biloba* and *C. grandiflorum*. Both are widely scattered over the sea-coasts of the tropics of both worlds. *I. biloba* is a sand-hill and shingle-beach plant (that is to say, it will grow among pebbles on a sandy beach). *C. grandiflorum*, so far as I have seen it, grows on broken rocks on the shore, or over bushes, not on sand. Practically all coasts and all islands have patches or large extents of sand, but broken rocks are far less abundant. There are none in the Malay Peninsula, wherefore *Calonyction grandiflorum* is absent; but there is plenty of sand on both coasts, wherefore *I. biloba* is common.

I. biloba has very long creeping stems, often over 30 feet long, and branching in all directions, so as sometimes to quite cover the sand-bank and hold the sand from shifting. It flowers well and produces plenty of seed. *I. carnosa* and *I. denticulata*, like *Calystegia soldanella*, have much shorter creeping stems, a foot or two long, and often grow in shifting sands. They are much less abundant, and consequently by no means so widely distributed.

Calonyction grandiflorum (*Ipomoea tuba*) is a seashore plant, widely distributed and sometimes very abundant, creeping over stony beaches. The seeds are nearly ½ inch across. It ranges from East Africa, Aldabra, Seychelles, Diego Garcia (Chagos), India, Ceylon, Maldives, Andamans, Little Coco, Mergui, Borneo, Java, Cocos-Keeling, Philippines, Krakatau, North Australia, Admiralty Isles, Cook, Fiji, Solomons, Pratas Isle (China), West Indies, Guiana, Fernando de Noronha.

The seeds float for 42 days, and Guppy has germinated them satisfactorily after 1 year's flotation in sea-water. He says, however (in the "Dispersal of Plants in Cocos-Keeling") that he found the capsule floated, but soon dehisced, and the seeds usually sank in 6 or 7 days, though 2 out of 9 floated for 6 weeks. They probably vary in buoyancy.

Calonyction muricatum.—This is another sea-dispersed species, but it is also cultivated for its swollen fleshy pedicels, which are eaten. It has a less extensive distribution area than the preceding, but it is found in West Africa, Cape Verde Islands, Angola, Zambesi, India. inland (probably introduced), Burma, Norfolk Isle, America from Mexico to Brazil, Fernando de Noronha. It is also a robust climber on broken rocks by the sea, and on bushes.

C. bona-nox, the Moon Flower.—This beautiful plant is now widely distributed all over the tropics, but it owes some of its wide distribution to cultivation, for it is a very popular plant in gardens. The seeds vary in floating power (according to Guppy), some sinking at once, some floating for months.

It is known from West Africa, including S. Thomé Island, Madagascar, Comoro Isles, India and Ceylon (doubtfully wild), Burma, banks of the Irrawaddy, Celebes, Timor, Lord Howe's Island, Polynesia to Hawaii, South America, West Indies, Cozumel Island, near Yucatan, Galapagos.

Hemsley (in "Flora of Lord Howe's Island," *Ann. Bot.* x, p. 45) doubts that this plant is wild anywhere but in South America, where, indeed, it seems to be common; but as it appears in the early collections of Cook's botanists (1768–1780) in the New Hebrides, Tonga and Tahiti, it is probably native in Polynesia. I should suggest that, originating in South America, it has been dispersed by sea as far as the Polynesian Islands, and perhaps West Africa.

Stictocardia (*Argyreia*) *tiliaefolia.*—A large climbing Convolvulus which, growing frequently on the seashore, is found also far inland up to 1,300 feet altitude in Southern India. As it is, however, a handsome plant, perhaps it has been carried by man to some of its inland spots. The seeds of the seashore form float readily, but Guppy says that those of the inland form do not. Like *Merremia nymphaeifolia* and *Operculina turpethum*, which also do not grow on sand-hills, but over rocks and trees a little way from the beach, the seeds are variable in buoyancy, and thus the dispersal area is more limited than in the case of *Calonyction*, in which all the seeds are buoyant.

Stictocardia, though widely distributed, is absent entirely from some areas where it might be expected. Thus it appears to be quite absent from the Malay region. It is found in West Africa, including Ile Principe, Cape Verde Isles, St. Helena, Mauritius, Seychelles, Comoro Islands, India, on the East Coast, in the Sundribuns and Madras, Andamans, Ceylon, Cambodia, Polynesia, to Hawaii, Western South America, Galapagos, Colombia. It seems probable that it reached America from Polynesia by sea-currents.

Operculina tuberosa.—This stout yellow-flowered Convolvulus is given in many books as having a distribution all over Asia, Africa and America. It seems to be, however, quite absent as a wild plant from Asia and Africa, and confined to Guiana and the West Indies, Martius ("Flora Braziliensis") says perhaps also Brazil. The fruit is normally a large round capsule surrounded by the leathery accrescent sepals, and 4 seeds closely appressed and forming a spheroid, each with a round back and erect facets, 1 inch in length. Sometimes only 2 are developed, and sometimes even only 1. In this case the single seed takes the form of the 4 seeds and is slightly furrowed. The testa is hard and dense, and there is a hollow space between the convoluted cotyledons which gives them buoyancy. It is only these abnormal seeds, the solitary ones, that float, the normal ones showing little or no buoyancy. Guppy says that of 3 of the abnormal seeds from the Jamaican beach-drift, Turk's Island and Shetland, 2, including the latter, floated in sea-water and sank in fresh water. They are, according to Hemsley, not uncommonly met with on the Caribbean beaches, and sometimes carried far up into the North Atlantic by the Mexican Gulf Stream. Guppy met them rarely in the beaches of Jamaica and Turk's Island, but they are said to be washed up commonly on the beaches of Cuba and South America.

The interesting thing about these seeds is their appearance on the coasts of Orkney and Shetland and the Hebrides. They are first described and figured by Clusius (Exoticorum Libri II, xvi, 41, fig. 9) in 1605, and they have been recorded by several authors as found in these islands as late as 1908 (Hemsley, *Ann. Bot.* vi, p. 69, pl. xxiv). No doubt the buoyancy of the seeds plays some part in their drift along the rivers from Mexico to the West Indies and Guiana, but as a sea-dispersed plant to distant countries it is a failure, as the only current which drifts these seeds away goes at once into the high north temperate zone, where the plant cannot grow.

O. turpethum.—This appears to be usually an inland plant, but Guppy says that in Polynesia it is also found flourishing at or near the coast. The seeds vary in floating powers from a few weeks to months, and it may have been conveyed from island to island by sea. It is widely distributed in the Old World, but as it seems to have had a medicinal value in early days, may owe some of its distribution to man. It is found in East Africa, Zambesi, Rhodesia, Madagascar, India, Sundribuns, Andamans, Nicobar, Assam, Ceylon (doubtfully wild, Trimen); Siam, Java, Philippines and Polynesia. It is quite absent from oceanic islands and from most of the Malayan region, except where man may have carried it.

Merremia nymphaeifolia (*Ipomoea peltata*).—A big climber with large yellow

flowers (rarely white) and large seeds. It does not grow (so far as I have seen) on the seashores, but usually inland, some little way from the coast. It is, however, undoubtedly sea-dispersed. According to Guppy, the seeds, like those of *Calonyction bona-nox*, are irregular in floating powers according to whether the seed fills the testa or not. He found the seeds floating in the drift of the Rewa River, Fiji, and says they float for weeks or months. The plant is found in Mascarenes, Malay Peninsula, Borneo, Java, Christmas Island, Celebes, Amboina, Fiji.

M. vitifolia.—This is often to be seen creeping along river banks, and I suggest from its distribution it occasionally travels by sea. It is found in the Mergui Islands, Andamans, Nicobars, India, Siam, China, Malay Peninsula, Borneo, Timor Laut, Amboina.

Calystegia.—This appears to be a genus of Antarctic origin, which has spread by its sea-dispersed seeds to the north temperate region. There are 3 species, *C. sepium*, the White Bindweed; *C. tuguriorium*, still confined to the Antarctic area, and *C. Soldanella*, the sea-sand Convolvulus.

C. sepium is a very well-known common plant in England, where it is chiefly an inland plant on waste ground, but sometimes, as Guppy points out, it is riparian, growing along the banks of the Thames, Kennet, and other rivers, climbing on reeds and river-bank shrubs. It spreads largely by its underground rhizomes, which are slender and white, and which can even pass through brick walls. In fact, it is often a great nuisance to gardeners. I have never seen it on seashores, nor have I any record of its having been seen there in Europe. It is found all over Europe, except the extreme north, in the Azores, and in North America, southwards to Chile, in Australia (1802), New Zealand, St. Paul's Island, Tristan d'Acunha, Japan and China. The distribution of the plant is very remarkable, not only as to the places it has arrived at, but also as to those from which it is absent. It appears to be absent from Africa, the Canaries, etc., and a great part of temperate Asia. It has undoubtedly been transported by man to some extent in the seeds, or more likely portions of the rhizomes in soil, but, I think, not largely. It is clearly not an abundant plant in the world, though it is very widely distributed, and it is very plentiful where it has established itself, very largely in these cases by its rhizomes.

The seeds (as Guppy shows) are variable in buoyancy, apparently from the differences in size of the kernel as compared with the testa. All seeds I have tested floated in water readily.

Though apparently, formerly at least, a sea-dispersed plant, as proved by its appearance on the shores of the Atlantic islands, etc., it has spread since its arrival in north temperate regions by river and flood, and by its underground rhizomes, having ceased to be a seashore plant. It is not known in a fossil state in Europe at all. *C. tuguriorum*, an allied species which much resembles it, is a native of Chatham Island, New Zealand, and the island of Masafuera, near Juan Fernandez, which locality it doubtless reached by the sea-transport of its seeds.

C. soldanella.—This is a sea-sand Convolvulus which to some extent plays the part of *Ipomoea biloba* in the temperate regions, but it is by no means so abundant a plant. The creeping stems are very much shorter, and consequently there are fewer flowers to a plant, and hnece the reproduction is slower.

It is found in the middle and south European shores (but absent from the Arctic regions), in China and Japan, on the Pescadores and Liukiu Islands, Tristan d'Acunha, California, Chile, Uruguay, New Zealand and Lord Howe's Island. It is absent from the Azores, Canaries, etc. It would be quite possible for this plant to be disseminated in ballast, but I have no evidence of this. The seeds are regularly sea-dispersed and about 30 per cent. will float unharmed for 1½ years, and 40 to 50 per cent. for 6 months.

Ipomoea biloba (*I. pes-caprae*), the Goat's-foot Convolvulus, is one of the most widely distributed of seashore plants. It is a long creeping plant on sand or shingle, but chiefly on the sandy beaches of all the tropics. It occasionally occurs inland, where sea-sand has been brought for ballast. I have seen it thus on railway banks in Kelantan, and on sand which had been brought from the sea inland in Negri Sembilan, both places in the Malay Peninsula. It is found in Cape Verde Islands, West Africa, St. Helena, Socotra, East Africa, South East Arabia, Persian Gulf, Madagascar and all the Mascarene Islands, Diego Garcia (Chagos), India (both sides), Maldives, Great Coco, Minikoi, Andamans, Mergui, Cambodia, Malay Peninsula and islands, including Cocos-Keeling, Christmas Island, Krakatau, Hainan, Formosa, Pratas Island, Australia, Polynesia, South America, West Indies, Fernando de Noronha. In fact, allowing for a few places where the ground is unsuitable for its development, it practically occurs all over the warm seashores in both regions. A little may be allowed for transport in sand-ballast, but it is clear that it has reached nearly all the localities mentioned by the drifting of its seed in the sea.

I. carnosa.—This little sea-sand Convolvulus has a wide dispersal, and its seeds are (as Guppy shows) readily transported by sea-current. It has rather a short creeping stem buried in sand, only the flowering shoots projecting. The seeds are hairy, but after lying on the sands for a year, they lose the hairs and are quite bare. Guppy tested the floating of the seeds, and found that after 3 months 20 per cent. of the hairy seeds of the year were floating, and all of the bare seeds of the previous year, and after 17 months 10 per cent. of the hairy seeds were floating. The survivors germinated freely, and from them he raised plants. Here it seems that the seeds improve in floating powers if kept for a year on a dry sand-bank; perhaps this is due to some contraction of the kernel, making them lighter. It occurs rather locally on sand-shores in the Azores, Morocco, Syria, Egypt, Naples, Angola, the Cape, in Ceylon, the Malay Peninsula, Tonkin, Hainan, Liukiu, Formosa, China, Hawaii, North America, in Mississippi and Louisiana and Lower California, West Indies, Guiana and Brazil. Millspaugh suggests its having been brought to the Azores in ballast, but Guppy considers it was brought by the Gulf Stream, as he found a sound seed of *Sapindus saponaria* from the West Indies on the same beach, and there seems no reason to doubt this.

I. denticulata (*I. littoralis*).—This is another little seashore Convolvulus like *I. carnosa*, which creeps in the sand and whose seeds are dispersed by sea-currents. It is found in the Little Coco (Andamans), Ceylon, Mergui, Siam, the Malay Peninsula, Labuan, Borneo, Cocos-Keeling and Celebes. Its distribution seems to be confined to the Malayan and Burmese region, and to have hardly extended outside this area.

I. campanulata.—A robust climber over rocks and bushes by the seashore (but not a sand dune plant), and also growing on river banks. In India it is found inland, but possibly planted or dispersed by floods from rivers. It is certainly, however, sea-dispersed, as in Malaya it is chiefly an island plant, and occurs in India, Bombay, and Madras, Ceylon, Burma, the Andamans, Penang, Pulau Adang (islands off the west Malay coast), Labuan, Borneo, Java, Christmas Island and the Philippines.

Many species of the order, besides these, have a very wide area of distribution, which cannot be attributed to sea-dispersal or to human agency, notably such plants as *Merremia umbellata* and *Aniseia martinicensis*, common on both sides of the globe. They are neither useful nor ornamental, nor do they occur on sea-coasts or in positions in which they could be drifted into the sea. Furthermore, they are conspicuously absent from islands. It is difficult to see to what they owe their wide distribution.

Cuscuta.—The dispersal of the Dodders to remote islands is very puzzling.

The seeds are very small, and Guppy finds that in the case of the Hawaiian endemic species, *C. sandvicensis*, and an introduced Fijian species, they sink at once, and he says that, as they absorb moisture very speedily, they are not likely to be bird-dispersed. We know that they are not rarely conveyed from place to place by human agency in seed or grain of cultivated plants, but this will not account entirely for their appearance in oceanic islands.

Thus we have in the Canaries 5 species, most, if not all, introduced by man, 1 endemic; Madeira, 1 or more; Socotra, 1 widely-spread species; Hawaii, 1 endemic species; Fernando de Noronha, 3 species, 2 Brazilian, *C. americana* and *C. decora*, and 1 endemic; and Galapagos, 2, *C. gymnocarpa* and *C. acuta*.

Guppy suggests that the seed may have been carried on floating logs, which is possible. The only Malay Peninsula species, *C. hygrophilae* (now identified as *C. obtusiflorus* var. *australis*, a plant occurring in China, Australia, etc.), certainly grew in the timber yards of Johor and in the town of Singapore only, and may have been introduced into these places accidentally by Chinese. But I am by no means clear as to how the endemic species originally reached the islands.

SOLANACEAE.

Physalis minima.—This plant is frequently found as a weed of cultivation, being accidentally carried about by man, and also dispersed by cattle which feed on it. It may also be dispersed by birds. Prain notes that in Little Coco (Andamans) it grew just above the spray line, and says he saw fruits in the sea-drift. They float from their bladdery calyx containing air. I found 3 forms of it in Christmas Island, a nearly glabrous erect form in waste ground —no doubt introduced by human agency—and 2 prostrate viscid pubescent forms near the sea on hot dry places and on rocks. Probably these latter were sea-dispersed forms. Lister found it there before any human being had visited the island. A species not unlike this viscid one grew in dry spots in Fernando de Noronha, *P. viscida*. Similar forms to those of Christmas Island occur in Australia, Lombok, Timor Laut, Java, and Madras. The common, tall subglabrous plant is certainly spread as described above, but the creeping or sub-erect viscid hairy form is, I suspect, dispersed by sea.

ACANTHACEAE.

In these herbs and half-shrubby plants the seeds are almost always ejected by explosion of the capsule, but in 3 or 4 species of *Acanthus* which grow in great masses in tidal mud-flats or tidal river banks the seeds are hardly ejected by explosion, and float readily in the sea. The capsule is oblong and contains 4 flat, elliptic thin seeds covered with yellowish processes, somewhat felted. In the remaining species of the genus, which are all terrestrial plants, the seeds are hard, smooth, thicker and glabrous, and ejected merely by explosion. The tidal-mud species are herbaceous plants with stems about 2 feet tall (one of them, *A. volubilis*, climbing on grasses and bushes), with prickly holly-like leaves.

A. ilicifolius grows in India, Sundribuns, Madras, Ceylon, Andamans, Malay Peninsula in the north, Siam, China at Macao and Hainan, and the Malay Islands as far as New Caledonia. *A. ebracteatus* is found in Siam, the greater part of the Malay Peninsula, Borneo, Celebes and Australia. *A. volubilis* in the Sundribuns, Malay Peninsula, Papua, Timor Laut, Australia and the Solomon Islands.

None of these had reached Krakatau by 1919, or occur on Cocos-Keeling or Christmas Islands. The plants, though growing in tidal swamps, mostly grow away from the sea, i.e., far up the rivers, and probably require more or less moving waters.

BIGNONIACEAE.

Dolichandrone Rheedii (*D. spathacea*).—The genus contains 9 species, all but one very local. Three are endemic in Australia, 1 in Portuguese East Africa, 3 in Southern India, 1 on the banks of the Irrawady River in Burma, and 1 in Lower Siam; the one above-mentioned, *D. Rheedii*, has an extraordinarily wide distribution from India to the Solomon Islands. They are all trees with long-tubed, white nocturnal flowers and long pods of winged seeds. The seed is central, with a pair of lateral oblong, thin hyaline wings, so that they are readily dispersed by wind, as is the case in almost every plant of the order. All but one grow in forests or woods inland, but *D. Rheedii* is a tidal-mud plant, frequenting tidal rivers or mud swamps by the shore. It most nearly resembles the Indian inland species in habit, foliage and flowers, but is especially closely allied to the river-bank Burmese species *D. serrulata*. From all the other species it differs in its seeds. Instead of having thin hyaline wings longer than the body of the seed, it has at each side a short oblong corky prolongation quite unsuited for wind-dispersal, and is quite unlike any other Bignoniaceous seed. When dropped from a height it falls straight to the ground, while the seeds of *D. serrulata* flutter in falling, rotating as they go, to a considerable distance. By the shortening and thickening of the seed-wing it has been adapted for dispersal by sea.

The tree is found along the west coast of the Indian Peninsula in Malabar and Travancore to Ceylon, and up to the Bay of Bengal on the east coast, along the coast of Burma and the Malay Peninsula, in the Andamans and Nicobars, and the Malay Islands from Sumatra to New Guinea, the Philippines and New Caledonia.

The story of this tree illustrates the great advantage in long-distance dispersal possessed by a plant whose seeds have been modified for sea-dissemination over those whose seeds are adapted for wind-dispersal only.

D. Rheedii is certainly derived from one of the genus with seeds modified for wind-dispersal, as those of nearly all of this large order are, and I should suggest it came from *D. serrulata* of the river banks of the Irrawaddy in Burma, as it so closely resembles this species in other respects that the two plants have been confused by some botanists.

It is easy to see how a riverside tree like this, gradually extending its area down stream till it came to the brackish water, could become adapted to a life in salt mud, and a concomitant thickening and reduction of the wings of the seed would convert it into a tree adapted for sea-dispersal. The reduction and thickening of the wing, it may be noted, cause the seed to fall direct into the water and prevent it from being blown away over the land, to dry unsuitable localities.

I found this tree a long way inland, in plains in Perlis, north of the Malay Peninsula. The ground on which it grew had, at no great geological distance of time, been seashore, but had been silted up, and was now covered by an inland vegetation. This littoral tree had adapted itself to circumstances, and was thriving many miles from the sea. It might in time, as the land pushes out more and more into the western sea, revert to a wind-dispersed form.

Though I cannot go as far as some writers in considering that a very large number of plants in the interior of islands, which have no longer any means of sea-dispersal, are the modified descendants of plants which originally colonised the islands by sea-transport, still, ir is quite possible that some of these plants owe their origin to the evolution of littoral plants.

The constant change from sea to land going on all over the world entails the isolation of littoral plants inland, and their consequent deprivation of salt. Many in this position perish, but others, if they could be modified so that they

can adapt themselves to the change of environment, may be so altered in various ways that they may be referred by us to distinct species. I believe this has happened in *Dodonaea*, in *Colubrina pedunculata* of Christmas Island, and in many other plants.

VERBENACEAE.

Vitex trifolia.—This plant has 2 forms, one a woody sand-creeper with simple round leaves (var. *repens*), and the other a bush or small tree, growing inland, with trifoliate leaves. Both forms are found in the same area, and plants of the creeping form which I brought from the sand-hills of the east coast of the Malay Peninsula developed into the bush form when cultivated in the Botanic Gardens, Singapore. The bush or tree form is known to the Malays as Lagundi, and is a popular medicine, and planted in gardens and village compounds. The plant is found in the Mascarene Islands, but probably only introduced there. It seems to be native in India, Madras and Bombay, Ceylon, Burma, Siam, Malay Peninsula, Java, Borneo, Celebes, Philippines, North Australia, and Polynesia to Hawaii. Penzig records *V. negundo* from Krakatau. I have not seen the specimen, but I should expect it to be *V. trifolia*, *V. negundo* not being a seashore plant.

Prain also records it from Little Coco Island (Andamans), but as it is sometimes cultivated, it may be only an escape there. The fruit is a small drupe, of which the outside is corky when dry. It is buoyant from the outside coat being light. Guppy found them in river-drift of the Rewa River, Fiji, and very abundant in the beach-drift of Hawaii. The fruit is also, he says, dispersed by pigeons, but certainly floats a long time, and probably owes its wide dispersal to sea-currents.

Clerodendron inerme.—A seashore shrub, usually a bush, but it is described as having a small trunk with long hanging branches, scrambling up rocks in Samoa. Unlike almost all other species of the large genus, the fruits of which are pulpy, often brightly coloured and distributed by birds, this plant has quite dry fruits consisting of 4 pyrenes, pear-shaped but flattened on the inner face. The outer rounded face of each pyrene is thick and corky-woody, and inside is a single seed surrounded by a thin woody testa (Pl. XIII, figs. 8 and 9). They float readily for a long time—many months—and the plant is the most widely dispersed species in the genus. It usually grows in tidal mud, but also among seashore rocks. It is found in India, in the Sundribuns and Madras, Ceylon, Andamans, Siam, Burma, Malay Peninsula and islands to New Guinea, including Aru, Timor Laut, Lombok, Krakatau, Christmas Island (a shrub I found here without flowers or fruit was, I believe, this plant), Australia and its islands, New Caledonia, New Ireland, Samoa, Fiji, Tonga, Hongkong, Liukiu Islands, Hainan, Formosa.

Premna integrifolia (*P. serratifolia*).—The plants of the genus *Premna* are shrubs or small trees inhabiting Asia and Africa, with very small globose black fruits, as big as a peppercorn, with a thin outer pulp covering a hard stone with from 2 to 4 cells, each containing a single seed, of which frequently only 1 develops. These little inconspicuous fruits are distributed by birds, and some species are thus carried to islands, e.g., *P. foetida*, a common Malayan one, to Krakatau; *P. lucidula*, a Javanese species, to Christmas Island. The greater number of the *Premnas* are inland plants, but one, *P. integrifolia*, is a habitant of muddy or dry sandy soils along the sea-coast. It varies from a low shrub to a medium-sized tree, and is variable in foliage. Guppy retains the name *serratifolia* for the inland form in Fiji, and *integrifolia* or *taitensis* for the littoral form.

The variety known as *taitensis* differs in appearance from *P. integrifolia*, of Ceylon and Malaya, in its much laxer corymb of flowers. The plant appears,

indeed, to be somewhat polymorphic. The fruits are about 5 mm. long, with a thin fleshy pericarp; the stone is very hard, bony and warted, with thick walls. It contains 2, 3 or 4 cells, of which only 1 contains a seed. These fruits float for a considerable time, their buoyancy being caused by the empty cells. Guppy compared the buoyancy of the inland form (his *P. serratifolia*) with that of the seashore form (*P. taitensis*), and showed that of the former 73 per cent. were 1-seeded fruits, 23 per cent. 2-seeded, and 4 per cent. 3-seeded stones; while in the seashore plant 92 per cent. were 1-seeded and only 8 per cent. 2-seeded.

The inland form had less buoyancy on the whole than the seashore form. Thus, as we see in many other cases, the wide distribution of the plant is due to the abortion of 3 out of 4 seeds in the fruit.

The species ranges from Madagascar, Comoro Isles, Seychelles, Aldabra, Mauritius, Diego Garcia to India, Bombay, Madras, Ceylon, Andamans and Nicobars, Siam, Tonkin, Formosa, Malay Peninsula and islands to Australia, and Polynesia as far as Fiji.

The original home of this plant was doubtless in the Indian or Malayan region, where the genus is very strongly represented, and it radiated thence by sea to the Mascarene Islands in one direction and eastwards to Polynesia in the other.

Guppy (in "Dispersal of Plants," as illustrated by the flora of Cocos-Keeling Islands) mentions the occurrence of drift fruits of *P. obtusifolia*, but this was probably *P. integrifolia*.

Avicennia.—This genus of about 9 very similar species of trees is exclusively confined to tidal mud, occurring in Mangrove swamps or on tidal rivers. The species are distributed all over tropical Africa, Asia and America, but are quite absent from Polynesia, as also from all islands unsuited, by absence of tidal river mud, for their growth, such as Cocos-Keeling, Krakatau, Christmas Island and Fernando de Noronha.

The fruit is a more or less flattened capsule, usually shortly tomentose or woolly outside, and containing 1 seed, which commences to germinate before it falls from the tree.

The following are the species and their distribution:—

Avicennia officinalis.—East Africa, Bombay, Madras, Ceylon, Andamans, Burma, Malay Peninsula and islands to the Philippines.

A. marina.—Red Sea, Jeddah, coasts of East Africa, Madagascar, Seychelles, Aldabra.

A. alba.—Sundribuns, Malay Peninsula and islands to New Guinea.

A. sphaerocarpa.—Siam, Penang and Philippines, and China.

A. lanata.—Singapore. *A. intermedia* (probably a hybrid between *A. officinalis* and *A. alba*), Malay Peninsula.

A. eucalyptifolia.—Timor, New Guinea, Australia.

A. balanophora.—Australia. *A. resinifera*, Australia, New Caledonia, New Zealand.

A. nitida.—West Africa and all the coasts of South America from Florida southwards, West Indies, Bermudas, Galapagos. *A. tomentosa* of New Guinea is very near this.

Here we have the typical sea-dispersal distribution again. The species of Asia range as far as East Africa and are absent from West Africa. Those of West Africa are identical with those of South America. The broken-up coasts of Asia and Australia possess a number of species, while there is but one (and a very closely allied if distinct species) in the whole of West Africa and both coasts of South America combined.

AMARANTACEAE.

Philoxerus vermicularis is a small succulent, prostrate ascending herb, common on sand-banks in the West Indies and all along the coasts of South America from Florida to Patagonia and West Africa. I found it in Fernando de Noronha, and it has been collected on Holbox Island, Bay of Honduras, and in Madeira. The small flowers are in heads of bracts, and the minute fruit is round and 1-seeded. It is no doubt sea-dispersed. It was very abundant in Fernando de Noronha, scrambling over the boulders on the shore, and also is found on the Cape Verde Islands and the Island of St. Louis. It seems clear that this fleshy plant is sea-dispersed, and probably by its very small seeds, though possibly by floating fragments.

Beta maritima, Sea Beet.—This common seashore plant, the origin of the cultivated beetroot, is a native of the coasts of Europe, the Mediterranean and Madeira to Palestine, Egypt and Persia, usually on sandy shores, but also in deserts in Egypt, and not rarely on rocks. Though truly littoral, in most places the fruits and seeds have little buoyancy. Thuret states that the dry fruits float for 2 or 3 days. Guppy found fresh fruits floated 1 or 2 days. Martins found the seeds lasted in a germinable condition for many weeks, and says the fruits floated, but it is doubtful that he means they actually floated for many weeks, or 40 days, as he says. Sernander says they drift from coast to coast. It is quite possible that whole plants or branches carrying fruit might be drifted for some way.

BATIDEAE.

Batis maritima.—A sea-marsh plant of South America, southern North America, and the West Indies. The fruit consists of a number of ovaries (8 to 12) with their bracts connate in a corky mass about ¼ inch long, each ovary containing a seed. The fruits become detached in sea-water and float for 1 or 2 weeks. Then they decay and set free the seeds, which germinate, as they float from 6 weeks to 3 months after the fruit decays, but (apparently) do not separate the cotyledons or extrude the plumule till they arrive on land (Guppy). The plant occurs in North America, both coasts of South America, and the West Indies, and is found in Margarita Isle off Venezuela, and in the Galapagos.

POLYGONACEAE.

Polygonum Raii (*P. Roberti*).—A littoral species allied to *P. maritimum*, if not a form of it. According to Praeger, the nuts float for over a month. They are large and smooth. This plant occurs on seashores in Europe, in Britain, Denmark, Sweden, France, Spain, Italy, in North America from Prince Edward Island to Vancouver, and along the Atlantic coast to Virginia.

P. maritimum is equally, or further, spread, and reaches the Azores and Madeira. Guppy writes :—" I have made observations on this plant in Devon-" shire, the Lipari Islands, and the coast of Chile... The fruits have little or no " buoyancy, but enclosed in the perianth they float for 3 or 4 days. The entire " plant floats, but portions placed in sea-water sank within 5 or 6 days," and he considers it is dispersed by wading birds. This may be so, as clearly many *Polygona* are so dispersed, but, as I show on p. 224, some of those which he affirmed to have non-buoyant fruits (*P. hydropiper*, etc.) undoubtedly are water-dispersed, and the nuts float for a longer period than he estimates.

LAURACEAE.

Cassytha.—There are about 8 species of these slender yellow parasitic leafless climbers with small drupaceous fruits in short racemes. All are natives of Australia (one also occurring in New Zealand), except a single species, *C. filiformis*, which is found on seashores all over the tropics, including many islands. (*C. capillaris*, a very slender plant occurring in Ceylon and Borneo, is apparently a local variety of it.)

To some extent the fruit is eaten and the seeds dispersed by birds. Those of the Australian *C. pubescens* are said to be sweet and eaten by children; those of the seashore *C. filiformis* are pulpy and white, though the pulp is thin in proportion to the size of the seed. Hemsley records the seed being found in the crops of pigeons. The seed of *C. filiformis* is, however, mainly dispersed by sea, hence its very wide distribution. The plant always grows parasitically on bushes close to the sea, covering them with a tangled mass of yellow wiry stems, growing equally well on sandy and rocky shores. It occasionally goes a short way inland. In Penang I have seen it attacking nutmeg trees some way from the sea-edge. In some of these cases the plant undoubtedly spreads inland by its climbing powers, scrambling on from bush to bush as far as it can go, and dropping its seeds farther and farther inland from its starting-point, till it is stopped by overshading or excessive moisture, or some such change in its environment.

Guppy records it growing inland in the rolling plains (Talasinga) of Vanua Levu, in the Fiji group of islands, but here it grows in company with *Cerbera odollam* and *Ipomoea biloba*, and it is clear that this flora must be the remains of an old sea-coast one left behind from the retirement of the sea. In Hawaii he has also found it growing inland in the lower woody region.

In most other parts of the world, at all events, it is quite confined to the sea-edge, and is undoubtedly sea-dispersed. The seed, which is quite small, has the same modification for buoyancy as we found in *Ipomoea biloba* and *Thespesia populnea*, etc., the incomplete filling of the testa by the cotyledons leaving an air-space. They float readily for some months. Perhaps, too, the whole plant bearing fruits may be dispersed, for Chamisso (in "Kotzebue's Voyages") writes :—"We find compact masses of *Cassytha* among objects "cast up by the sea" (in Radack).

The plant doubtless took its origin from Australia (as all the other species occur there only), and is now found on the coasts of that country and the Polynesian Islands, all the Malay Islands (though absent from Cocos-Keeling and Christmas Island), including Krakatau to the Malay Peninsula, Siam, Cambodia, Hainan, Hongkong, Pratas Island, Bonin and Formosa, Mergui, Andamans, Ceylon, Madras, Madagascar and all the Mascarene Islands, including Amarante, East Africa to Arabia and West Africa, also Florida, West Indies and South America to Brazil, but absent from Fernando de Noronha. It appears to have radiated from Australia to Polynesia, to the Chinese coasts via the Philippines, and to the Malayan coasts, and via Ceylon to East Africa.

HERNANDIACEAE.

Hernandia.—A genus of seashore trees, in which the round, hard woody fruit is enclosed in the much enlarged calyx. In the most common species, *H. peltata*, the calyx forms a fleshy cup covering the fruit, except at the top. In *H. ovigera* the yellowish-white calyx is 2 or 3 inches across, a globose bladder with an opening at the top. The black globular-ribbed fruit is much smaller, and situated at the bottom of the bladder. When the whole is placed in the water, it floats erect, and the fruit acts as a weight so as to balance the calyx

in the water, so that, however much it is tossed about by the waves, it remains upright and no water enters at the hole in the top (Pl. XIII, figs. 5 and 12).

This species is less abundant than *H. peltata*, but occurs in Bombay, Diego Garcia, Java, Christmas Island, Amboina, Celebes and New Guinea.

H. peltata occurs in Madagascar and Mascarene Isles, Madras, Ceylon, Andamans, Laccadives, Maldives, Minikoi, Diego Garcia, Mergui, Malay Peninsula (rare), Java, Sumatra, Borneo, Labuan, Krakatau, Philippines, Australia and neighbouring islands, Admiralty, Solomons, Cook Islands, Fiji, Pitcairn Isle.

There are several other species, 1 in Australia, 1 in New Caledonia, 1 in West Africa and one, *H. sonora*, of South America and the West Indies.

The buoyant tissue of the fruit is said by Schimper to form a layer between the hard outer coat and the seed, and apparently in *H. peltata* the soft enlarged calyx plays no part in the buoyancy, but certainly in *H. ovigera* it acts as a boat to carry the fruit, which forms a ballast to steady the boat. As it floats high in the water, it is possible that wind aids to drive it along the sea, as happens in the case of *Spinifex* and *Gyrocarpus*. The fruits float for months—Guppy says 42 days. It is possible that the evolution of the calyx into the fleshy cup covering the fruit was destined for bird-dispersal, but I have no evidence that birds eat it. *Cryptocarya* (*Laurineae*), in which the calyx forms a thin layer over the fruit when ripe, is regularly dispersed by birds.

Gyrocarpus americanus (*G. Jacquini*) is a big soft-wooded tree with fruits about ½ inch long, terminated by 2 narrow spathulate papery wings, like those of a *Dipterocarp*. They are formed of 2 sepals, the tube of the calyx adnate to the nut In many places this is an inland tree, the fruits being merely dispersed by wind as in *Dipterocarps*; but the trees frequently grow on river banks, so that the fruits blown into the stream are carried away, and they often grow near enough to the sea to be drifted in by the streams, or even to be blown by wind into the sea. Here they float for a long time, and the plant has thus a very wide dispersal.

Several species have been described, but all seem to be forms of one, except a very curious small species, *G. habaliensis*, found in desert regions in Eritrea, East Africa, probably an evolution of the common one.

The tree is found in East Africa, Rhodesia, Madras, Bengal, Little Coco, Penang, on Pulau Badak, Pulau Adang off the Malay coast, Mergui, Buru, Timor, Timor Laut, Christmas Island, Australia, Fiji, Samoa, Tonga, Mexico and Costa Rica.

Guppy found that the fruits could float unharmed for 2 months in sea-water, and that the wings, which float only a day or two by themselves, actually lessened the buoyancy of the fruit. Of fruits with both wings attached, 40 per cent. floated after 2 months, while of those with the wings cut off, all floated as long. In the course of the flotation the wings in most cases break off during the first few weeks, and in the sea waves probably sooner. I have certainly seen them floating in the sea, with the wings on, off Pulau Adang, near the Malay Peninsula. The wings of the fruit have served their purpose when the fruit is blown into sea or river, and though their projecting tips may serve as sails in the wind, to carry them up river or off the shore, as I have noted in *Dipterocarpus*, for long-distance floating they would not much assist. When the tree is in fruit it has shed all its leaves, and the fruits, exposed to the wind, hang down on the ends of the branches. In Christmas Island the tree (called the Cabbage Tree by the settlers on account of its soft wood resembling a cabbage-stalk in texture) grew to a very great size on the coral terraces over the sea.

Guppy is surprised at its comparatively local distribution in the Polynesian Islands, but this seems to be everywhere its habit. It does not occur anywhere on the mainland of the Malay Peninsula, though it does on two outlying islands,

nor is it at all common in the Malay Archipelago. In Christmas Island it is abundant near the shore, and I found a spot covered with young plants in thousands, about 6 or 8 feet tall. It is difficult to see why it should be so local, but the same remarks, as far as the Malay Peninsula is concerned, apply to *Ochrosia borbonica*, *Tournefortia argentea*, *Hernandia peltata*, which, with *Gyrocarpus*, are hardly ever found in this area, except in Pulau Adang, a group of islands lying off the west coast of the Malay Peninsula. *Cordia subcordata* and *Pemphis acidula* also occur only in a few spots, chiefly islands in this area, yet fruits and seeds of these plants must frequently have been stranded on the coasts and on other islands in the neighbourhood, but have failed to establish themselves.

EUPHORBIACEAE.

Euphorbia.—A large genus abundant all over the world. The fruits are tricoccous, explosive, ejecting the small or minute seeds to some distance. Very many are small weedy herbs, in some of which the seeds have been largely dispersed by man, carried in soil or grain or other seeds, and some possibly conveyed in mud on the feet of birds or mammals. Like all these small-seeded plants which grow in open spots, the seeds are also dispersed by rain-wash; a small number are undoubtedly sea-dispersed, and probably some others.

E. hirta (*E. pilulifera*), a plant growing now as a weed very abundantly all over the tropics, both on seashores and inland, reached Krakatau and Lang Island by 1899, and is the only distinctly weed-like plant of that date there. Endemic species of this genus occur in Ascension Island, *E. origanoides* (allied to and possibly an evolution of *E. Atoto*), *E. Heleniana* of St. Helena, *E. ramossissima* of Pitcairn and Elizabeth Islands, *E. Chamissonis* of the Marshall Islands, and 14 or more species endemic in the Galapagos islands, besides *E. hirta* and *E. thymifolia*, possibly introduced.

Euphorbia Paralias, the Sea Spurge of the English shores, is one of the species undoubtedly sea-dispersed. The small seeds float unharmed for a long time in the sea. Guppy states that they may commonly be seen in drift along the southern coasts, and he has seen them in Sicilian drift. They possess a layer of spongy tissue containing large air-spaces between the kernel and the hard testa, by which they float, but neither the hard testa nor the kernel float of themselves.

Like several other sea-dispersed plants of temperate regions, the Sea Spurge has but a small distribution area compared to tropical species. It is found in Europe from Ireland to Greece, and as far north as Holland, Tunis, Egypt, Morocco, and the Canaries and Madeira. Like *Honckenya* and *Crambe maritima*, it has failed to reach the Azores.

Euphorbia atoto.—This takes the place in the tropics of *E. paralias* in Europe. It grows in sandy and even muddy spots. According to Guppy, the seeds float at most but a few weeks, and the buoyancy is due to their possessing spaces in the fold of the cotyledons, which do not fill up the testa. A totally different method of flotation to that of *E. paralias*.

The probability is that its floating powers vary, and that some seeds can float for a long time, for, as will be shown, not only is its distribution very wide, but it is a plant very characteristic of island littoral floras. It is found on the shores of Madras, Ceylon, Andamans, Nicobars, Maldives and Laccadives, Malay Peninsula, Siam, Cambodia, Hongkong, Pratas Island, Formosa, Liukiu, all the Malay Islands including Timor Laut, Christmas Island, Krakatau, to New Guinea and the Philippines, Admiralty Islands, Australia, Louisiades, Fiji, Solomons.

Aleurites moluccanus, Candle-Nut.—This tree is widely scattered all over

Asia, but it has long been valued for its oily nuts, used for illuminating, and has been carried about and planted all over the tropics. It is commonest in the Polynesian Islands, but Guppy seems to think it has been introduced there. I have never seen it wild in any part of Malaya, and it is clearly not a native of India or Ceylon. The seeds are often to be found on beaches in Polynesia, Java and Cocos-Keeling, but, according to Guppy, always empty or with a decayed seed. Sound seeds are only to be found in beach-drift at the mouth of estuaries, where they have been freed from fruits brought down by the rivers. The fruits will float, but only for a week or a fortnight. The tree occurs in the uninhabited Kermadec group of islands, but Guppy suggests that the Polynesian islanders visited these islands and took it there. It is certainly absent from Krakatau and Christmas Island. Keating records it on Cocos-Keeling Island, and Chamisso as drifted on the Java coast, in a germinating condition. The tree is probably not sea-dispersed at all, but has simply been carried about by man.

Ricinus communis, Castor Oil.—This plant probably originated in Africa, and has been carried all over the world and planted for the oil seeds. According to Guppy, the seeds, which he has found in beach-drift, sound and decayed, can only float from 5 to 10 days. They are recorded by Keating as drifted upon Cocos-Keeling Island, and the plant appeared in Krakatau, undoubtedly from sea-borne seed, in 1919. Copeland found it floating in the sea off South Trinidad. Martins kept seeds floating for 93 days in sea-water, and afterwards raised plants from them. The seed is furnished with a dense testa, which apparently protects it from the action of the water. I have never seen or heard of it as a seashore plant.

Hippomane mancinella.—In this tree the fruit has an inner coat of air-bearing cork-like tissue. It is round and hard. Guppy kept some floating for 5 weeks in sea-water, and thinks they will float for months. The tree grows on both coasts of South America, West Indies, and southern North America. The fruit, poisonous as it is said to be, is eaten by goats. It resembles, when fresh, a crab-apple, and will float with the flesh on, but is more buoyant when the flesh has dried off in the sun by lying on the beach. It contains 6 loculi and usually 3 seeds.

Omphalea.—A genus of shrubby climbing or tree *Euphorbiaceae* with large 3-seeded fruits. Most of the species occur in the West Indies, but 2 are found in the Philippines and Borneo, 1 in Australia, and 1 in Madagascar.

O. diandra.—Guppy says of this plant: " The seeds of this must be recorded " as typical of the West Indian beach-drifts." They are black semi-globose, 1–1½ inches across, and possess a hard crustaceous shell. They are characteristic of the Trinidad beaches, and were collected by Morris on the coast of Jamaica. About half of the seeds collected by Guppy on the West Indian beaches contained kernels. The kernels float, the buoyancy being due to the lightness of the albumen, but also partly to a shrinkage cavity between the cotyledons. The plant is a river-bank climber extending from the West Indies and Central America to Peru and Brazil.

O. triandra has similar seeds and floats readily. It occurs in Jamaica and Guiana, and the seeds also on the beach-drifts. This plant is a tree. The testa is thinner than in *O. diandra*. There is a large cavity between the cotyledons, and the kernel is buoyant. Both of these plants are inland species, not littoral, and the buoyancy seems more suited for river than sea-dispersal. The Old World species are quite distinct from the American ones, though somewhat resembling them. Of the American species, 8 are West Indian, 4 are found on the mainland, and 1 in Brazil. They are mostly recorded as seashore or sand-hill plants. The Madagascar one is also littoral.

The headquarters of the genus is certainly the West Indies and eastern

South America. The remarkable distribution of the Old World species suggests that the genus was once much more extensively represented, and was probably sea-dispersed, but has died out in most of the Old World.

Excoecaria agallocha is a tidal-swamp tree with small tricoccous fruits, the seeds of which float for months, having a buoyant tissue inside the testa. A widely-distributed plant, but absent from many unsuitable localities, especially islands, as it is a plant characteristic of muddy or sandy-muddy tidal swamps. It is found in Bombay, Madras, Sundribuns, Ceylon, Mergui, Andamans, Malay Peninsula, Cambodia, Hongkong, Formosa, Liukiu, Malay Islands from Sumatra to New Guinea, including Krakatau (1919), Australia, Caroline Isles, New Caledonia, Fiji, and other Polynesian Islands. There can be no doubt that this widely dispersed tidal-river tree owes its distribution to sea-dispersal.

CASUARINACEAE.

Casuarina.—The She-Oaks are lofty trees with long, pendent, leafless jointed branches and small, more or less oblong cones with persistent lanceolate woody bracts, which open like a bivalved capsule and let out a small indehiscent winged nut about ¼ inch long. The wing of the nut is terminal, or nearly so, and lanceolate. The nuts are shaken from the pendent cone and drift away on the wind like any other samara, and in the headquarters of the genus, Australia, where they grow in open country, this seems to be their only method of dispersal. But there are several species outside Australia, in New Caledonia, Fiji, Borneo, and the Philippines, which have probably reached these spots by sea-dispersal, the method by which the most widely dispersed species of the genus, *C. equisetifolia*, has been diffused along the coasts of tropical Asia and East Africa. The trees, which are often 100 feet tall, grow on sand dunes, a short distance above high-tide mark, often in a single line, though sometimes, as on the shores of Kelantan, east coast of the Malay Peninsula, they form a kind of open forest. On the coast of Borneo, near Santubong, I have seen them forming a line at a considerable distance from the sea-beach, but here the sea has receded a long distance since the time the trees first sprang up and established themselves, and so they were left inland. The tree is very commonly planted for its timber and firewood, both in the interior of the Malay Peninsula and in India, but in a wild state it is confined to sea and river sand flats. I found seedlings coming up on sand-banks on the island Pulau Rawei, off the west coast of the Malay Peninsula. There was one adult tree on Pulau Adang, about ½ a mile away, but none on Rawei, much too far for the seed to be blown across by wind, and these islands are 24 miles from the nearest land, the island Terutau, and 50 miles from the mainland, and I have no record of the plant growing on either.

The tree occurs in a wild state in North Australia, Polynesia, Fiji, Samoa, Marquesas, Solomon Isles, in the Malay Archipelago on Rawak, New Guinea, Philippines, Little Kei, Aru, Celebes, Landak, Java, Cocos-Keeling, Banca, Krakatau, Sumatra, Malay Peninsula (both coasts, but chiefly the east), Tenasserim, Andamans, Diego Garcia, Madagascar, Mascarene Islands including Aldabra, East Africa, Usambara, Rovuma Bay, Zanzibar, Namaqua and the uninhabited Europa Islands.

In Siam, Keith found a clump at Bangtaphan by the beach, but near a temple, perhaps introduced. It was in St. Helena by 1868, but probably planted.

The tree appears to be quite absent, as a wild plant, from India and Ceylon, the Chinese coast and islands, and the Laccadives, Maldives and Minikoi. Probably in these islands the seashores do not suit it. It occurs patchily along

the coast of the Malay Peninsula, Borneo, etc., the groves or lines of it being often many miles apart.

Guppy says the seeds only float a week or two, but I do not think this can be so always, as it is clear that the tree can cross extensive areas of sea. It is not carried about by natives, though Europeans frequently plant it, so that in most, if not all of the localities given, the plant must have got there by sea.

MONOCOTYLEDONES.

AMARYLLIDACEAE.

Crinum asiaticum.—This fine large *Crinum* inhabits sandy, and more seldom rocky, coasts of tropical Asia, and is far the most widely-spread species in the genus, if not of the order. It has a large bulb and short, thick fleshy stem, usually about 2 feet tall, and a number of long flaccid leaves, from the axil of which rises a tall peduncle bearing a large umbel of white flowers. The fruits are more or less globular or pear-shaped, with a thin irregularly dehiscing pericarp, and usually 1, more rarely 2, seeds. The solitary seed is usually rounded, flattened at both ends, and 1 to 2 inches across, though they vary a good deal in size and form. Outside there is a thin fleshy, leathery testa. The bulk of the seed, however, consists of a large mass of light albumen, usually green and pithy in texture. The embryo is small. When the fruit is ripe, its weight bends the peduncle down to the ground, the pericarp breaks up, and the seeds fall out, all on the plant falling together in a mass and being washed away by the tide. That such soft seeds should be able to float unharmed for long distances in the sea is very remarkable. Guppy affirms that they sink in a week or two, but, as the plant is very characteristic of distant islands, it is quite clear that they must be able to float for a very much longer time unharmed.

The plant is found on both coasts of India, Ceylon, the Andamans, Mergui, Pulau Mohea on the west Siamese coast, Trang, Malay Peninsula, and the islands from Sumatra to the Philippines Islands, including Krakatau (1919), Christmas Island, Aru, Timor Laut, Australia, Fiji, also Hainan, Formosa and Japan.

In Christmas Island I observed that plants often grew in the hollows of the coral rocks, far from the sea at the present time and at a great height above it, suggesting that the ancestors of these plants were there at the time when these upper reefs, now inland, were close to the sea. In some cases, however, the plant had slowly moved upwards to a great height above the sea in this way: when the plant is growing at the foot of the cliffs, the tall 4-foot peduncle with ripe fruit falls against the cliff, and some of the seeds drop into the hollows worn in the coral-reef cliff, where a little soil has collected, and here the plant grows, now 4 feet higher up the cliff than the parent. It again drops its seeds, some at least, 4 feet higher into upper hollows, and so the movement goes on till the plant has reached the top of the precipice. The peduncles which face the sea drop their seeds into the water or on the shore, where they drift away to other parts of the island, or farther away, or sometimes into the woods below, where they usually fail to establish themselves.

An allied species to this, and probably an evolution of it, is *C. Northianum*, which grows in tidal mud, in rivers and streams in Sarawak, Borneo, and in Kedah and Kelantan in the Malay Peninsula. It differs chiefly in producing long stolons in the mud, and in having much larger fruits. The seeds are doubtless dispersed by the tidal streams.

Many of the other species of *Crinum* have similar seeds, though usually

rather smaller, and inhabit low-lying fields and swamps, where their seeds are dispersed by floods.

C. defixum, a smaller species than *C. asiaticum*, grows on turfy pastures by rivers in India, Ceylon, Burma, the Malay Peninsula and Borneo, where the seeds can be diffused along these marshy spots by the rise of the river.

C. americanum.—This I suppose to be the *Crinum* mentioned by Guppy (in " Plants, Seeds and Currents," p. 15) as flourishing at the water's edge in the Black River, Jamaica, " its large fleshy seeds frequently occurring in the " germinating condition in the river-drift." It occurs also in Florida. Possibly the seeds may drift along the coast, as do those of *C. asiaticum*, though to a small extent.

C. asiaticum is a very popular plant with the ubiquitous hawk-moth, *Sphinx convolvuli*, so that when in flower this moth may be certain to appear, if anywhere within miles. When the plant on Christmas Island (during my stay there) flowered, I caught 4 of these moths on it the first evening the flowers opened, showing the immense distances these moths can fly across the ocean.

Pancratium maritimum, a seashore species of the Mediterranean coasts, has small black, more or less angled seeds which seem light enough to float. They are about ¼ inch long. Arcangeli (in " Sulla Struttura et Disseminazione dei Sami da *Pancratium maritimum*," Bull. Soc. It., 1895, p. 278) suggests that as these black seeds are very conspicuous lying upon the sand, they might be mistaken by birds for beetles, and so carried off and dispersed, which is extremely improbable.

TACCACEAE.

Tacca pinnatifida.—A herb with a large tuber and tall leaves. Flowers numerous on a tall peduncle, fruit oblong or ovoid baccate, with a large number of small seeds. These seeds have a spongy testa by which they float for many months.

The plant grows in sand on the seashore, and is very widely distributed. In some places, Polynesia and Africa, the tuber is used for food to a large extent, and this accounts for its wide occurrence all over Central Africa, and perhaps to some extent for its abundance in the Polynesian Islands. In the intermediate area it is rarely, if ever, used for food, and is not planted.

It is certainly wild on the east coast of Africa, Zanzibar, Usambara, and is reported common by Lake Nyassa. It is widely spread over Central Africa to the west coast, probably by human introduction. It is found in Madagascar, Comoros, Seychelles, India, Bombay, Maldives, Laccadives, Minikoi, Ceylon, Andamans, Cambodia, Malay Peninsula, Pahang on the east coast and Pulau Redang; Pulau Besar and Lankawi Isles on the west coast, Malay Islands to the Philippines (absent from Krakatau, Christmas and Cocos-Keeling Islands), Australia, Polynesia.

PANDANACEAE.

Pandanus.—The Screw Pines are widely diffused and abundant all over tropical Asia, Polynesia and tropical Africa, on the mainlands as well as the islands. They are quite absent from the New World. They are not known as fossils in Europe with any certainty, the fossil remains attributed to this genus being only dubious fragments of leaves.

A large number of the species known are inhabitants of forests or inland situations, where they cannot be dispersed by sea or river action. Many, however, are abundant on river banks or in rivers, and some are habitants of sea rocks and beaches.

Of the inland species, some have the fruit pulpy and coloured red or yellow, and these are probably dispersed by birds or mammals. The plants are almost

always unisexual, though sometimes part of the bush or tree produces male and part female flowers.

The fruits consist of woody 1-seeded drupes closely packed in a cylindric or globose head. In some species the drupes are separate, but in others several —2 or more—drupes are connate into a single mass (*syncarp*). These large, usually woody syncarps are detached from the rachis when the head breaks up, and can usually float. Where the drupes are not connate into syncarps they are detached separately. Ripe fruits are, however, not readily met with except in a few species. Male plants, especially in the jungle species, are rare or quite unknown, and the female plants of these never seem to produce fertile fruits. Out of 30 species of *Pandanus* in the Malay Peninsula, of 22 the male flowers are quite unknown, though of some of these I have seen 100 or more female plants. Of some, e.g., *P. parvus* and *P. ornatus*, which are common plants in the south of the Peninsula, I have only seen single male plants and never ripe fruits. These seem only to be propagated by fallen branches. Those which have male and female flowers on the same clump (*P. kaida*, *P. samak*, *P. atrocarpus*) fruit readily and commonly. A certain number have pulpy coloured fruits, and are certainly, I think, disseminated by birds or mammals, the drupes or syncarps being not too large to be swallowed by large birds or carried off by rats or squirrels. Such are the jungle *P. Houlletii*, of Singapore, the drupes of which are pulpy, sweet, and of the flavour of pine-apple, and *P. Kaida*, of Siam, with soft red syncarps. There are also some epiphytic species in the Malay Peninsula, Sumatra and Borneo, the fruits of which (mostly unknown) must be transported from tree to tree by birds or bats.

Guppy considers that the distribution of the inland *Pandani*, which are extremely local in Polynesia, as indeed they are in the Malay forests, must have been dispersed by birds in spite of the large size of the fruits, which would require the aid of larger birds than now exist, and points out that the Mascarene Islands, which were the home of the large ground-pigeons—the Dodo and Solitaire—are tenanted by an unusually large number of *Pandani*. He has not seen pigeons eating the fruits of these plants, neither have I. Locally these fruits may be dispersed, after falling, by rats or land-crabs.

P. helicopus, a very large, much-branched tree of the forest rivers of the Malay Peninsula, Sumatra and Banka, where it forms vast, dense thickets in the river, often blocking the waterway, has cylindric heads of separate drupes of a dull green colour, 5 inches long and 3 inches through, the separate drupes being only ¼ inch through. These heads, on falling into the water, float, till the drupes become detached and float away. They are used by the Malays as baits for fish-traps, whence I conclude that fish eat them and probably pass the hard stone of the drupe, by which means the plant may be conveyed from river to river by fish. The red pulpy syncarps of *P. Kaida*, which grows in or near water, also float, the whole head, over 1 foot long, falling into the water, where it breaks up.

There are, however, a number of plants in which the large woody syncarps of several drupes are found on the seashores and are undoubtedly sea-dispersed. The most widely distributed and typical of these is *P. fascicularis* (*P. odoratissimus* or *P. tectorius*). This is a bushy species about 10 feet tall, usually much branched. The whole head of fruits is about 8 inches through, the separate syncarps of several carpels 2 inches long, obconic and red. They are very fibrous and float readily. The plant grows on seashores from India, Ceylon, Malay Peninsula and Islands, including Maldives, Laccadives, Minikoi, Nicobar, Krakatau, Australia, South China, Liukiu Islands, Bonin, Marshall Islands, Radak, Tahiti, Hawaii. It is absent from the whole African region, and is replaced by *P. Andamanensium* in the Andamans, *P. Leram* in the Nicobars,

and *P. nativitatis* and *P. elatus* in Christmas Island, and *P. Forsteri*, allied to *P. nativitatis*, in Lord Howe's Island. To the same set of *Pandani* also belong *P. Seychellarum*, of the Seychelles, and *P. Heddei* and *P. Kirkii*, of East Africa.

The drupes of *P. fascicularis* are abundant in sea-drift all over the Indian and Pacific Oceans, and are cast up on Cocos-Keeling Island, where the plant has not established itself. This *Pandan* grows to a certain extent inland, where the soil is suitable, as on the plains of Fiji, between the sea and mountains, and is also carried inland by natives, who use it for thatch, baskets, hats, etc., and in some places eat the fruits (Polynesia and Nicobar). Guppy considers it a human introduction to Hawaii, but it is possible that it has sea-drifted there.

The peculiarity about these plants is that those growing in distant islands are sufficiently distinct to form what are, botanically speaking, species. The 2 Christmas Island species, though obviously sea-dispersed, as their fruits drift about in the sea around and are washed up high on the cliffs, are quite distinct from the common Malay seashore plant, and from each other. If we assume that all these island plants are descended from or are modifications of the typical seashore species, the plant must vary very readily. Very few species of this section of *Pandanus* habitually occur far inland. One of these is *P. Klossii*, which is confined to the plateau of Gunong Tahan, in the interior of the Malay Peninsula, at 5,000 feet elevation. It is really very much like *P. fascicularis* in many points, and has no relation to any of the *Pandani* growing in the immense stretch of forest between it and the sea. This plateau is formed of a hard sandstone of great antiquity, which there is some reason to believe has formed at the mouth of a large river which formerly took its rise in Borneo, perhaps in Miocene times. If this is so, it is easy to conceive this plant as being derived from a primitive form of *P. fascicularis*, which grew on the sands of the old river mouth and has persisted ever since.

It may be mentioned here that, owing to their unisexual habits and scarcity of male flowers, and the difficulty of making satisfactory herbarium specimens, this group of plants is by no means well known. Many of the 156 known botanical species are based on absolutely inadequate material. They can only be satisfactorily described from plants growing wild, and this has seldom been done.

FLAGELLARIACEAE.

Flagellaria indica.—This is a wiry tough climber which scrambles over bushes near the sea by the aid of its tendrilled leaves. The fruits are less than ¼ inch through, globose and pink. The outer layer (exocarp) is thin and soft, the mesocarp woody, extremely hard, containing a single seed which completely fills the space, but there are 2 very minute empty spaces in the hard shell, the remains of the other 2 cells of the ovary. The fruit floats, at least in the dry state, though I doubt if these tiny spaces have any effect on its buoyancy.

The wide distribution of this plant and its abundance on seashores certainly suggest that it owes its dispersal to sea-transport rather than to birds. All the species of the order *Flagellaria* and *Joinvillea* appear to have originated in Polynesia. *Joinvillea* is not a seashore plant, but a reed-like plant with a bright red 2- or 3-seeded berry, and abundant in Polynesia to Borneo and the Malay Peninsula, doubtless transported by birds. *Flagellaria* has more inconspicuous, pale-pink fruit and a single seed, and has spread from Polynesia through Indo-Malaya to the Mascarene Islands and Africa on both coasts. The African form, *F. guineensis*, is very closely allied to the Asiatic one, if indeed really distinct.

F. indica inhabits muddy spots by tidal rivers or edges of Mangrove swamps, where it climbs on trees or bushes. It ranges from New Ireland, Lizard Island, the Solomons, "covering the shores of a rocky islet," North Australia, New Guinea, the Philippines, Celebes, Java and other islands, to the Malay Peninsula,

Siam, Hainan and Formosa, India, Sundribuns, and Ceylon, Andamans, Madagascar, Mauritius, Bourbon, Seychelles. Another species occurs in Samoa and Fiji, and *F. guineensis* in tropical Africa. It is absent from Cocos-Keeling, Christmas Island, and Krakatau. More information on its habits is required, but I think that its distribution, structure, and buoyancy of the fruits strongly suggest that it is sea-dispersed, though birds may play some part in its dissemination.

PALMAE.

Cocos nucifera, the Coco-Nut.—The origin and history of the Coco-nut Palm have been frequently discussed by botanists. The latest *résumé* of the information on this subject has been compiled, with critical remarks, by O. F. Cook, in the "Origin and Distribution of the Coco-Palm (Contrib. U.S. National Herbarium, vii, ser. 2, p. 1). The original home of this now ubiquitous Palm appears certainly to be in Costa Rica and Panama. The Spanish traveller Oviedo visited Panama in 1515 and published his "Natural History of the Indies" in 1526. In this work he writes :—"These Palms or "Cocos are tall, and there are many on the coast of the southern ocean in the "province of the Cacique Chiman, and many in that which they call Borica, "and many more than in both places in an island of the southern gulf, which "is in the ocean 100 leagues or more from the coast of Peru." Burica Point is a peninsula of Costa Rica, lat. 8·1 N., long. 82·55 W. I cannot find any island corresponding to the one he mentions.

Cuz de Leon (1532 to 1550) mentions an isle of Palms 25 leagues south-east of Cape Corrientes. This may be Gorgona Isle. Dampier (1686) records these Palms as growing from Ecuador to Mexico. Acosta mentions seeing them in San Juan de Porto Rico in 1570 to 1587.

A very interesting note is given by Peter Martyn (in "Hakluyt's Voyages," v, 381). The voyage, he described, took place in 1520. He describes the Coco-nut (*Coccus*) occurring in the Maluchas Islands (Moluccas) quite accidentally. Later he is writing about Panama. He says : "In those countries there is "a great plenty of the fruit of the *Coccus*, where, especially on the south coast, "the flowing sea washeth the broad neighbouring playnes, of the which they "say one is overflowed by the floud for the space of two leagues, and becometh "dry again with the ebb. In these places (they say) those trees grow and "increase of their own nature, and not elsewhere, unless the young and tender "plants be transported thence. Some think that the flowing of the sea brings "the seeds thither from unknown countries of the Indies, where they naturally "grow. They say they are brought to Hispaniola and Cuba, as I some time "said of the trees which bear *Cassia fistula*, and from the islands to the continent, "until they come to those Southern parts."

I find no mention of any explorer of that date finding Coco-nut Palms in the West Indies or on the Atlantic coasts of South America, and do not quite understand his allusion to Hispaniola and Cuba, unless he means that the fruits have drifted there. The description of the plains flooded by sea-water for 6 miles at high tide, and forming the original home of the Coco-nut, is very remarkable.

Hernandez said the Coco-nut was in the Philippines in the 16th century, but was not disseminated on the Atlantic Ocean till the discovery of America. The Coco-nut was, however, abundant in tropical Asia long before that time, which has caused some botanists to imagine that it was of Asiatic origin.

Seemann (in the "Flora Vitiensis") quotes from Goodwin (in the "Parthenon") a reference (in an inscription 1650 B.C.) to a Palm, Mama en Khanent, in a garden, which Brugsch suggests might be *Hyphaene argun*, but in the first "Sallier papyrus in an apostrophe to Thoth," he is described as

"Thou palm tree 60 cubits tall, on which are Kuki (fruits) with Khanini "(probably kernels) within the Kuku with water in the Khanini." ("Kuki" is a word constantly used by Pliny for a Palm, and is probably the origin of the word "Coco.") This early inscription and papyrus may refer to the Coco-nut, which it well describes. Seeman, however, suggests it may refer to *Borassus aethiopum*, but the water in the kernel of that is very little, if any, and the conspicuous mention of water in the kernel would really only apply to the Coco-nut. If this is the Palm intended, the reference is the earliest known to the Coco-nut.

Evidence for Sea-Dispersal of the Coco-Nut.

Though there can be little doubt that the wide distribution of the Coconut is due very largely to human agency, still there is considerable amount of evidence that the tree has been dispersed by sea-transport of the fruits.

J. Flygaer (*Linn. Amoen. Acad.*, viii, 1) mentions among fruits drifted up on the coast of Norway, *Cocos nucifera*, which grew successfully when planted. These fruits, like the *Cassia fistula* in the same list, were evidently jetsam from some ship. However, we have no record since of Coco-nuts floating to Europe in this way.

F. Leguat, in 1690, landed on Rodriguez Island, where there were no inhabitants, and found no coco-nuts on it, but some fruits were washed up in a state of germination soon after, which he and his companions planted, and the trees grew.

Guppy dealt with the question in his "Dispersal of Plants," as illustrated by the flora of Cocos-Keeling Island (Victoria Institute, 1890). He shows that in 1729 Jan de Marre saw the island covered with Coco-nuts and no inhabitants there, and the island was known as Cocos Island by the early Dutch explorers. There is no reason to believe it was ever occupied by settlers till Hare and Ross settled there in 1827. Keating mentions the drifting ashore of Coco-nuts of Bali, known by their shape and size, on the island in early days before 1836.

Mr. Clunies Ross informed both Mr. Guppy and myself that foreign varieties of Coco-nuts often drifted to the shores of the atoll, which he thought came from the South Seas, and some began to germinate and others established themselves, but the crabs often destroyed the germinating nuts. Early explorers found the islands full of myriads of sea-birds, which have now disappeared. Is it not possible that in those days these birds kept the crabs in check and so permitted the Coco-nut seedling to grow?

The destruction of the shoots of germinating seeds by crabs is probably the cause of the failure of the Palm to establish itself on many beaches, coasts and islands.

Cook makes a great point of its not having established itself on the Australian coast. Nuts have been found on the Queensland beaches, as well as husks and shells of fruits brought by Polynesian or perhaps Malay wanderers. Moresby and Dampier found the tree in abundance on the coasts of New Guinea and on the islands of Torres Straits. It is known that Malays visited the Australian coasts and took Coco-nuts with them before the country was discovered by Europeans, and as it is their constant custom to plant Coco-nuts on any shores they visit, it seems clear that on the Australian coasts the plant failed to establish itself without the protection of man.

The Coco-nut in all stages of its growth has many enemies: crabs, rats, pigs, eat the young shoots; coco-nut beetles, *Oryctes* and *Rhyncophorus*, destroy the buds; squirrels bore into the nuts and eat the contents. Any of these animals might completely prevent the plant from establishing itself on any locality.

In Christmas Island there were only a few trees of recent planting on the beach at the settlement when I was there, but I was informed later that more were found near where a stream entered the sea on the other side of the island, a spot quite unknown previously to the Europeans, who certainly had not planted the Coco-nuts there. It is possible, however, that some runaway coolie had brought them to the spot. The island, however, is an unlikely one for the plant to establish itself on naturally. There is no sandy beach, and few spots where the plant could grow. The cliffs all round are too high for it to be thrown up by waves, and the island abounds in crabs, and formerly in myriads of rats, which would probably destroy any germinating seed.

All the Maldive and Laccadive Islands and those surrounding these groups bear Coco-nuts, cultivated or wild, says Willis, and he seems to think it probable that they originally arrived at the islands by sea without human assistance.

Gill, in describing the uninhabited island of Nassau in 1862, records the discovery of a single Coco-nut Palm there.

Marco Polo mentions Coco-nuts in Samara (Sumatra), Nocueran (Nicobar), Angaman (Andamans), and in Madras and Malabar in 1280. I have seen carvings clearly representing this tree, together with those of *Borassus*, in the temple of Angkor Wat in Cambodia, built in the 11th and 12th centuries.

According to Bretschneider, it is mentioned in a Chinese poem of the 11th century B.C. It is mentioned as occurring at Santiago, Cape Verde Isles, in Drake's voyage of 1585, but not mentioned in the West Indies or Guiana in any voyages of the same date in Hakluyt.

It is quite clear from these writers that the plant was plentiful in the Old World long before the discovery of America, and it appears that at that time it was confined to the west coast of the Isthmus of Panama and the adjoining coasts and islands.

The fact that no other species of the genus *Cocos* or of any Palm allied to it is known from any part of the Old World, and the fact of its being found in abundance on the west coast of South America when the first explorers reached it, make it quite certain that it did not originate in the Old World.

The question then arises as to how it spread to the Old World, whether by sea-drift, or by human agency.

Cook disputes strongly the possibility of its drifting by sea. He states that few Coco-nuts could reach the water by falling from the trees, but as the nuts falling from a high tree can readily roll down the sandy shores into the water, and, indeed, often do so, there is no difficulty in this. The large 4-angled fruits of *Barringtonia speciosa*, when fallen, are regularly drifted away by sea, and they, from their shape, cannot roll like a coco-nut.

He says the thick husk, so characteristic of this plant, is necessary to permit the heavy fruits to fall from the tall trees with safety. But it is noticeable that no fruit which is not sea-dispersed possesses a thick husk like this, and we have similar thick fibrous husks in *Barringtonia* and *Nipa*.

The Durians, very heavy fruits, which fall from trees much taller than Coco-nut Palms, are not so protected. None of the inland species of *Cocos* possess a husk like this, and there can be no shadow of a doubt that it is only destined for floating the fruit from place to place in the sea.

He states that the Coco-nut seldom grows in the immediate strand overhanging the water, or even in reach of ordinary waves, which is exactly the place where they grow best. He seems, too, to have strange ideas as to the delicate nature of the seedling. If kept too moist, he says the nuts rot, and if too dry, they lose the power of germination; if allowed to lie in the sun, they are killed, and if under much shade, the seedlings make little growth. As a matter of fact, they are usually hung up in the sun to germinate. It is not rare to find

nuts shipped to England in holds of ships, piled up anyhow, germinating on their arrival in England. He suggests that very few cast up by the waves would avoid being smothered by bushes on the shore. If so, what chance would the regular seashore plants have of sea-dispersal, *Ipomoea biloba*, *Casuarina*, *Barringtonia*, *Scaevola*, etc. ?

He urges that the fruits of *Lodoicea* have often been drifted to the Maldives, and never established themselves anywhere out of their one locality, but *Lodoicea* is not a seashore plant. It grows in damp inland valleys, and could not grow on a sea-beach.

Prain, in his paper on plants of Coco Island, Andamans, states that after the Coco-nut Palm had arrived, it spread of itself: "Even toward the centre "of the island one meets with groves containing from a score to several "hundreds of trees from nuts which have been floated by unusually high "tides and left stranded far from the coasts."

The most important piece of evidence as to sea-transport of the Coco-nut Palm without any aid by man is that of its appearance at Krakatau after the vegetation was destroyed by the eruption. Trees appeared on Lang Island in 1897, and on Krakatau and Verlaten Island before 1906, and by that date were laden with fruits. Further, as some of the seedlings from the trees were as much as 3 feet tall (one metre), it is clear that the Palms had been established for some years. Ernst points out that there was a complete absence of the seashore crabs, which destroy so many of the seedlings of strand plants, which no doubt accounts for the successful growth of the Palm there. Van Leeuwen gives a good photograph of a seedling of the Coco-nut growing on the shore of Krakatau (in his paper in the *Annals of the Buitenzorg Gardens*), on the later development of the Krakatau flora. In his account of the vegetation of Sebesy Island he mentions finding Coco Palms on inaccessible cliffs where it was impossible for them to be planted by man, as the coast is never visited, and is inaccessible to native praus.

The Dispersal of the Coco-nut by Human Agency.—As has been shown, it is certain that the Coco-nut originated on the shores of Western Central America, and from thence spread to Polynesia and so up to tropical Asia. It was not introduced to the east coast of America and to the West Indies till about the 16th century. Martyn, quoted by Sloane, says it reached the Antilles about that date, and Acosta met with it in Porto Rico in 1570 to 1587. It was carried across the continent by the Spaniards, and was later conveyed to West Africa.

The Palm is strictly a seashore plant, requiring some amount of salt to thrive. Indeed, salt is frequently given to Coco-nut Palms in cultivation. Both in Brazil and in the East Indies the natives constantly affirm that the plant will not grow more than 20 miles from the sea, and though it will grow to some height in swampy or wet ground, it will never flower there. Strictly speaking, it will sometimes grow with success farther inland. I have seen it farther than 30 miles inland in Ceylon. Cook states that it flourishes at Bangalore, 200 miles from the coast, at 3,000 feet elevation, and Palmer states that thousands are grown in dry regions of Colima, Mexico, far inland. Ciezo de Leon saw it very abundant 23 miles from Cartago (Costa Rica) and 12 miles from Azerma, on a plain between two small rivers, but he describes the occurrence of lakes and pools of salt water in the neighbourhood of Cartago. However, it is clear that the Palm was unable to cross the Isthmus of Panama without the aid of man.

In what way it reached the Polynesian Islands from the coast of America is not clear, but I suggest that it arrived there by sea-drifted nuts. From these islands it spread to the Malay region in very early days, perhaps some thousands of years ago, by human agency as well as by sea-drift.

The Coco-nut is largely carried about in boats by travelling Malays and other sea-coast tribes, as a supply of water and food, and they have a habit of planting them on uninhabited islands or anywhere they stop, for a future supply, and in the neighbourhood of the Malay Peninsula they frequently claim rights to an island on the ground that the Coco-nuts thereon were planted by some ancestor. Polynesians and Malays have long been travellers by sea to very long distances in their sailing boats, and frequently, too, the boats of these seafaring folk have drifted long distances by accident.

G. Clunies Ross, of Cocos-Keeling Island, stated that he had found a drifting boat, with a crew, 200 miles away from Cocos Island, which had come from Java. He also told me that two canoes had arrived at Cocos Island, one of which contained a living boy whose language no one could recognise, even in Java, where the Dutch, who took charge of him, were well acquainted with the East Asiatic languages. In the other boat were two corpses. From the form of the canoe and other facts it seemed clear that these boats came from no Malayan island, but probably from some Polynesian one.

Besides by the accidental drifting away of canoes blown out to sea, the island folk for perhaps many thousand years have travelled by sea along coasts and islands of the Pacific and Indian Oceans, often for very great distances for trade and piracy.

The Macassar fleet regularly each year sailed to Singapore from Celebes, a distance of 1,200 miles, certainly as late as 1900, bringing all sorts of eastern island produce. There is little doubt that the Indonesian (Malayan) seafarers travelled as far as Madagascar and established themselves there. Coco-nuts would commonly be carried by these maritime folk, and no doubt frequently planted by them along their routes.

The common name for Coco-nuts among these peoples is "Niu," or variants of the word. In Tahiti "Niuh," in other Polynesian islands "Nu," etc., in Malay "Niur," in Nicobar Islands the same, in Madagascar "Wua Niu" (i.e., Buah, fruit, Niu, coco-nut in Malay).

On this Cook and others have based the idea that the fact of the name of the plant being the same from Tahiti to Madagascar, proves that the tree was only introduced by man from one place to the other. It is, however, no proof at all, as we find names of other seashore plants, which were certainly never conveyed by man, identical in both spots. Thus the word "Vintan" or "Bintan," *Calophyllum*, and "Waru" or "Baru," *Hibiscus tiliaceus*, are as widespread as "Niu," and used all along the route. These people, finding in their travels plants which they knew before, merely used their old names for them. Andrews, in Christmas Island, asked his Javanese the native names of the various trees, and though they had often never seen them before, at once they gave him names for them which were really the names of Javanese trees they thought they most resembled.

There can be no doubt that the Coco-nut owes a very large part of its distribution to human agency, but it certainly has also been sea-dispersed to some extent, for it is difficult to see how it could otherwise have come from western South America to Polynesia. Still, there appear to be very few other plants which have been sea-transported along the route. There is very little of the American flora in Polynesia. The only sea-transported plants in both areas are *Dioclea violacea*, *Mucuna urens*, and *Rhizophora mangle*, but these are enough to show that there has been a current from the continent to the islands by which the Coco-nut could have travelled. It may, then, have travelled by sea through the Malay region to the Andamans, Maldives to Madagascar, and possibly to East Africa, the same route as taken by *Barringtonia speciosa*, going gradually from island to island, but it is more probable that its journey from isle to isle was at least very much accelerated by human transport.

Beccari (in the "Original Dispersal of the Coco-nut," *Phil. Journ. Sci.*, xii, 27) suggests that the plant originated in Asia or Polynesia, and considers that the husk was developed as a protection from the Robber Crab (*Birgus latro*) which in Polynesia is known to attack the fruits. Both of these theories seem to me to be out of the question. *Cocos* has no affinities with any plant of the Old World (though he does allege that the Palm *Jubaeopsis*, of South Africa, is a member of the *Cocoineae*), and it is extremely improbable that the husk is developed for protection from the crab, which by no means always accompanies it, and occurs in other islands, e.g., Christmas Island, where there were no indigenous Coco-nuts, nor would this account for the similar husk in the Nipa Palm fruit.

Nipa fruticans.—This striking Palm is now confined to the Indo-Malayan region, ranging from the Sundribuns of Bengal to Ceylon, the Andamans and Nicobars, the Malay Peninsula and the islands to the Philippines, Australia, and the Solomon and Caroline Islands. In Eocene times it inhabited Europe as far north as Sheppey, Bracklesham, West Wittering, and Christchurch, South-East France, Belgium and Italy (Verona), South Russia and Cairo, and fruits have been found fossil at Grenada, Mississippi, in North America. In the latter locality the few fruits found may have been sea-drifted from Europe, and those of Belgium and Italy seem also to have been sea-dispersed. Some of these fossil Nipa fruits (*Nipadites*) are hardly distinguishable from the present-day species, though the most common form, *N. Burtini*, is larger than those of *N. fruticans*. Accounts of them are given by Rendle ("Revision of the Genus Nipadites," *Journ. Linn. Soc.*, xxx, 143), Bonnet (*Bull. Mus. Hist. Nat. Paris*, x, 1904, p. 499), and others.

The Palm is a creeping tidal-mud plant with a gigantic branching, almost fleshy rhizome (half buried in mud) which throws up large tufts of pinnate leaves 20 feet long. Great clumps of these rhizomes, with the projecting leaf-bases attached, are often broken off, and can be constantly seen drifting along with the currents in Malayan seas. The plant grows exclusively in tidal rivers or in deposits of tidal mud, often fringing the river banks in abundance for long distances. The fruits are flattened, ovoid or obovoid nuts, about 6 inches long and 3 inches or less wide, but vary very much in size and form, according to their position in the head (Pl. XIII, figs. 1 and 4). The head of fruits is dense and globose, 8 inches or more through, borne on a short stout peduncle. The fruits are shining dark brown, with an outer husk of fibrous tissue about 1 inch thick. The seed is enclosed in a hard bony testa, fibrous outside. The albumen resembles that of a Coco-nut. There is a small empty space in the centre, but the buoyancy of the fruit is due, as in the Coco-nut, to the light husk. When ripe, the fruits fall off the head into the water or on the mud, and on the rise of the tide are drifted away. Blume states that the seeds are not detached till the germination is so far advanced that the sea-water cannot injure the seedling. However, as the radicle and plumule are extruded at the base of the nut, where it has been in contact with the stout rachis of the head, they do not appear till the fruit is actually detached and lying on the mud or in the water. Floating seeds, with the plumule and radicle protruding from the base, are very common objects on the Malayan seas and shores.

The fruits drift about in the currents till they are thrown up in the mouth of a tidal river or on a muddy bank, where they can grow. The great detached masses of rhizomes may possibly be stranded in tidal rivers and continue to grow occasionally, but I have seen no definite evidence of this. It is highly probable that they may convey small tidal-swamp seeds and rhizomes, as well as insects, lizards, etc., to remote islands or distant coasts, as a large part of the leaf-bases project above the water in their drifting, and are not submerged. The distribution of the plant is, however, mainly due to sea-transport of the

fruits, and seems to depend on the presence of large tidal rivers bringing down plenty of mud. It is therefore not to be expected to occur on small oceanic islands, and, indeed, does not occur there. Fruits were found washed up in abundance on the shores of Krakatau by Ernst in 1906, but none have established themselves, and Guppy records them as drifted up on Cocos-Keeling Island also. They were abundant in the low-lying soil of the Economic Gardens, Singapore, now 4 miles from the sea, but where there must have been a tidal creek at some time.

Very few other Palms, if any, owe their dispersal to sea-currents. *Manicaria saccifera*, a tidal-river Palm of South America, has round seeds which, when sound, do not float to any distance, but dead seeds have been actually carried as far as Scotland and the Hebrides (Sloane, " Voyage to Jamaica," ii, 4, p. 186). The plant is confined to the east coast of South America, Panama, Guiana, Brazil, and has reached Trinidad.

Phoenix paludosa is a tidal-swamp Date Palm which occurs in the maritime swamps of Burma, Cochin China, the Andamans, and the north of the Malay Peninsula. The fruit is perhaps transported by birds swallowing it and passing the seed, but its distribution suggests that it may also be drifted to some extent.

As Beccari notes, Palms, with the exception of the Coco-nut and Nipah, are very little sea-dispersed, and usually absent from islands. Some few Palm fruits have been found floating in drift. Guppy records the drifting of dead stones of *Acrocomia* sp. to many of the beaches of Jamaica, Trinidad, Grenada, and as far as the Azores. These Palms are inland inhabitants of Brazil. He found empty seeds of the vegetable ivory, *Phytolephas macrocarpa*, in the Guayaquil drift. The sound seeds did not float, and the seeds of *Astrocaryum* found in the Panamas sea-drift were also dead. Off the Solomon Islands he found the fruits of the Betel-nut, *Areca Catechu*. This Palm is not known in a wild state, but is probably Malayan in origin. Moseley found a germinating fruit of *Orania aruensis* on the beach of Aru, and Beccari records finding uninjured fruits of this Palm thrown up by the sea on some of the islands. It is a local plant which may, however, be spread by sea to neighbouring islands.

Caryota mitis is, according to Prain, very common on the Andamans, on Narcondam, Coco Island, etc., and was probably introduced by sea. The fruit is dull red and not too large to be swallowed by birds, which I believe is the way it is disseminated in the Malay Peninsula, where it is the most common Palm. The peculiar Palm *Arenga Listeri* of Christmas Island, has small juicy red fruits containing 3 seeds, and is doubtless bird-borne, but it is endemic and not related to any other species known to me. Other island Palms are *Pinanga Manii*, of the Andamans and Nicobars ; *P. Kuhlii*, of the Andamans ; *Ptychoraphis augusta*, *Corypha macropoda*, *Licuala spinosa*, and some *Calami* and *Daemonorops*, in the Andamans ; and *Bentinckia nicobarica* of the Nicobars, in all of which the fruit is drupaceous, often red-coloured, and not too large to be swallowed by birds or fruit-bats, but Palms are decidedly rare in oceanic islands.

CYPERACEAE.

Mariscus Dregeanus, a sand-Sedge with a bulbous stem-base, common on sand of the seashore. This is probably sea-dispersed, as it occurs on many sea islands, and Willis and Gardiner seem to consider it certainly sea-dispersed in the Maldive Islands. It is abundant all over Africa on both coasts, and inland in sandy spots, but most common on the east coast. It is also found in the Seychelles, Comoro and Aldabra Islands, Madras, Bengal, Ceylon, Maldives, Minikoi, Burma, Siam, Malay Peninsula and Borneo.

Mariscus albescens.—A large and tall tufted Sedge, common on seashores of tropical Asia, from East Africa, Seychelles, India (both coasts), Maldives, Laccadives, Minikoi, Ceylon, Andamans, Mergui, Malay Peninsula, Cochin China, Hainan, Christmas Isle, Malay Island to Papua and Philippines, Tonga, Cook Isles, Samoa.

M. rufus (*M. ligularis*).—This species represents *M. albescens* in South America and West Africa, meeting the latter species in the Mascarene Islands. It has the same rough tufted habit, but the spikelets are smaller and in more cylindric racemes. Like the last, it is a typical seashore plant, not found inland. In South America it ranges from Florida southwards on both coasts, to Brazil and the West Indies, and is frequent on islands, including Cozumel Isle and Roatan Island, in Honduras Bay, Island of Margarita, off Venezuela, Galapagos, and in Africa, Madeira, the West African coast, Galega Island, Diego Garcia, Amirante, Seychelles, Aldabra.

Thus the two species together practically encircle the world in the tropical regions. They seldom go out of reach of salt, though I found *M. rufus* some way from the seashore in Fernando de Noronha.

M. albescens appeared in some quantity in a pasture-land saturated with salt water, owing to the breaking of a bund in Province Wellesley, Malay Peninsula, probably washed in by the rush of sea-water some years before, and a plant came up on a piece of coral reef brought probably from Rhio to the Botanic Gardens, Singapore, and built into a wall. It remained for some years growing from a depression in the coral rock.

M. brunneus, a seashore plant in America and the West Indies, is probably also sea-dispersed. It is found in Mugeres and Holbox Islands in Honduras Bay.

M. appendiculatus is the name given by Clark to the plant described by Hemsley as *Cyperus atlanticus* of South Trinidad, and the plants described by me as *C. Noronhae* and *C. brunneus* and in part *C. ligularis*, in the flora of Fernando de Noronha, which he says are the same thing. The original type plant came from Ascension Island, and it does not appear to be known from any other locality than these three islands.

All this set of seashore Sedges are very closely allied. It might be possible for the nuts of the island species to be borne attached to the feet of birds, or that they might be transported in cracks in pumice or floating timber; but though, as Clarke points out, the nuts of *Cyperi* and *Marisci* usually sink in water, the nuts (achenes) of these inland plants must be somehow sea-dispersed, and possibly float. They are rather corky, and the glume is thick, firm and usually ribbed, holding rather closely to the achene, and the latter may float enclosed in it.

Penzig mentions *Mariscus umbellatus* (*M. sieberianus*) as found in Krakatau at an early period. Van Leeuwen, however, says his plant was *M. albescens*, but in 1919, says he found *Cyperus cyperoides* and *Kyllinga monocephala* there. The former name appears to be intended for *C. cyperodes* Kurz, a name for *Mariscus Sieberianus*. This plant and the *Kyllinga* are common weeds of cultivation, and have no means of flotation. Neither occur in any oceanic island except in association with man, though very common and widespread species. I can only think that, like *Eleutheranthera*, the achenes were accidentally brought with the baggage of a previous expedition or possibly floated over in drift logs.

Remirea maritima, a Sedge creeping in sand, with a long rhizome. It is found on the sea-coasts of both hemispheres from South India, Ceylon, Mergui, Malay Peninsula and outlying islands, Pulau Tioman, Pulau Adang, etc., Cochin China, Siam, China, Malay Islands, including Krakatau, to the Philippines and Australia, South America, West Indies, West Africa, Madagascar

and Seychelles. It is absent from Northern India, Maldives, Laccadives, East Africa and Polynesia. There is no doubt of this plant being sea-dispersed. Its absence from many localities must be attributed to its requirements of stretches of sand. The small achene is oblong, thick, obscurely trigonous and smooth, and doubtless floats. The glume, however, wraps it very closely, and is thick and ribbed, and it may float in the glume.

Fimbristylis spathacea and *F. cymosa*.—These two tufted, wiry Sedges are widely distributed on sea-coasts of the tropics, growing on sand or rocks. They seem to be quite distinct species, though somewhat similar, and they occupy different areas of the world. *F. spathacea* ranges from the coasts of East and South Africa, Arabia, Socotra, the Mascarene Islands, India, Maldives, Ceylon, Malay Peninsula, Borneo, Java, Cocos-Keeling and Krakatau, Formosa, Hongkong, South America and the West Indies, and *F. cymosa* is found in Polynesia, North Australia and Christmas Island.

From their presence in oceanic islands it is clear that both plants are sea-dispersed, but it is rather remarkable that we should find only *F. spathacea* in Cocos-Keeling Island, 700 miles from Java, and *F. cymosa* in Christmas Island, which is really nearest to Java. Clarke gives *F. cymosa* as a Javanese plant, but I have seen no specimens. If it is not Javanese, the nuts must have drifted to Christmas Island from North Australia. The West African form is *F. glomerata*, a more robust form, which Clarke includes in *F. spathacea* (Clarke, however, seems inclined to class all three as varieties of one species). It occurs in Diego Garcia. It is difficult to account for the distribution of these species unless they are local forms of one widely dispersed species which has crossed both the Pacific and Atlantic Oceans.

Scirpodendron costatum is a tidal-mud Sedge forming large tufts of long rough leaves looking like a *Pandanus*. The fruits are about ½ inch long, acute, brown and corky outside, with a stony nut inside. The nut sinks, but the thick corky covering causes it to float. Guppy notes that the detached fruit is perforated at the base through both coverings, so that the water penetrates it readily, and soon causes sinking or germinating. He observed that stranded fruits were frequently to be found germinating on sandy beaches where they could not grow. This rapid sinking is an advantage to fruits stranded in a suitable locality, but a disadvantage to fruits requiring to be drifted long distances.

It is necessary, indeed, that fruits of such a plant, in which the spike of fruits stands up in the midst of a large bush of taller foliage, should have some means of drifting away, and not being lost in the mass of leaves, but it is really of little advantage that it should be drifted away from its tidal swamps, with the risk of being stranded on a beach useless for its growth. Many others of these tidal-swamp and riparian fruits are adapted for speedy sinking, before they are carried away too far by currents. Guppy found that 40 per cent. of the fruits sank in sea-water in the first fortnight, 15 per cent. floated after 5 or 6 weeks, and all sank in 2 months. These were from plants growing in Mangrove swamps. Those found in inland swamps were much less buoyant, some sinking at once, others floating for a week or two, the outer coat having largely lost its buoyancy. He has recorded many instances of this. As he says, the fruit is not adapted for dispersal by currents over long tracts of ocean. It seems to me to be one of that class of plants, not rare in tidal-swamp vegetation, which creeps by short stages along coast-lines or along a line of islands, and so has attained its rather long course of distribution. In spite of the size of the clumps of leaves, it is very easily overlooked by collectors, as it does not flower or fruit conspicuously or frequently, and it is extremely likely to be mistaken for a clump of some narrow-leaved *Pandanus* in a young state. It was so overlooked for a long time in Ceylon, and I have been deceived by it

myself. The fruits are eaten by some kind of rat, as I have often found them gnawed and carried off. Thus they are also dispersed by these animals. The plant is abundant in Fiji and Samoa, and occurs in Australia, Philippines, Amboina, Java, Borneo, Sumatra, Malay Peninsula, as far north as Setul, and in Ceylon. Its nearest point to Ceylon, where we know it grows at present, is in the island of Siberut, off West Sumatra, 1,240 miles distant.

GRAMINEAE.

Paspalum vaginatum, a widely-dispersed tidal-mud grass with a slender rhizome. There is some evidence that this is dispersed by the adhesion of the grains to the feet of wading birds. They might also be drifted on logs or in pumice, or the rhizomes attached to floating Nipa clumps or tree roots. It is possible that several of these methods of dispersal may be the cause of its wide distribution. It is found in South Europe, chiefly Southern France and Spain, but undoubtedly accidentally introduced. It is native on the coasts of East and West Africa, and the Cape, Madagascar and the Mascarene Islands, India, Andamans, Ceylon, Siam, Cochin China, Formosa, Malay Peninsula and Islands, New Zealand, New Caledonia and Polynesia, West Indies, Brazil, Peru. It had arrived at Krakatau by 1919, but is absent from Cocos-Keeling, Christmas Island and Fernando de Noronha.

Coix Lachryma-Jobi.—Guppy records finding fruits of Job's Tears floating in the sea off the Solomon Islands. Its floating powers are recorded under Dispersal by River (*see* p. 194). I have no record of any sea-dispersal of this grass.

Ischaemum muticum.—This grass grows on seashore mud and sand, creeping along or, when it reaches bushes, half scandent and tall. It is very common on all coasts from India to the New Hebrides. The flowers are in spikes. The spikelets, as usual in these plants, readily break off, and the outer glumes enclosing the grain are smooth and stiffly coriaceous, and can thus protect it when floating in the sea. It is found in Southern India, Ceylon, Burma, Maldives, Laccadives, Minikoi, Little Coco, Malay Peninsula, Cochin China and all the islands of the Malay Archipelago, including Krakatau (but not Cocos or Christmas Island), Admiralty Isles, Australia, New Caledonia and New Hebrides. It seems to be quite absent from the Polynesian Islands farther west, and has never reached the Mascarene Islands.

Spinifex squarrosus.—I have dealt with this under Wind-Dispersal, as the heads of spikelets are blown along the surface of the water to a surprising distance, and currents play apparently little part in its dispersal (*see* p. 37).

Thuarea sarmentosa, a prostrate creeping grass forming a mat of bright green leaves on seashore sand. The flower spike is short, and consists of a short, flat, broad rachis with 4 to 6 male spikelets and 1 female spikelet at the base, all on the lower side of the rachis. When the fruit is ripening, the male spikelets fall off and the rachis curves over the female spikelet so as to enclose it, and then becomes thick and bony, forming with the enclosed spikelet an irregularly oblong body ½ inch long, which, when detached from the plant, can readily drift away in the sea. Miss M. Niewenhuis Uexkull describes and figures the evolution and structure of this curious body (in *Ann. Bot. Gard. Buitenz*, 1902, XVIII, ii, 114), and Kurz (Journ. Bot., 1875, n.s., iv, 332) also describes and figures it under the name of *Ornithocephalochloa*, the complete "fruit" with the two ends of the detached rachis resembling a bird's head (Pl. XII, figs. 13, 14 and 15). Miss Uexkull collected her specimens in Java, where she studied the evolution of the fruit, and sent to Switzerland a number of them to try floating experiments. The experimenter tried floating 50 of them in water

from Zurich Lake to which had been added 70 gr. of salt (artificial sea-water), and 50 in fresh water from the lake. She found :—

In sea-water, of 50 fruits—			In fresh water, of 50 fruits—		
Sept. 30th	floated	29	Sept. 30th	floated	11
by Oct. 26th	,,	14,	Nov. 21st	,,	2
which floated till December 16th.					

Here it is shown that over 50 per cent. of the fruits floated readily in sea-water, and about half of these were still floating $2\frac{1}{2}$ months later, when the observations ceased; but in fresh water 22 per cent. floated at first, and only 4 per cent. still floated after 2 months.

The plant is not uncommon in tropical Asia, but is most abundant on islands. It is found in the Nicobars, Laccadives, Great Coco, Maldives, Minikoi, Ceylon, Malay Peninsula on both coasts, and on the outlying islands of Pulau Adang, Pulau Redang, most of the islands of the Malay Archipelago (absent from Krakatau, Cocos-Keeling and Christmas) to the Philippines, Bonin, Pratas Isle, Australia, New Caledonia, New Hebrides and most of the Polynesian Islands. Trimen points out that the fruit is pushed under the sand during ripening. It is easily swept away by wind and rolled into the sea with the sand, and so floats away.

Sporobolus virginicus (*S. pungens*).—This sea-sand creeping grass is widely distributed, ranging from Spain along the Mediterranean to tropical Africa, Ceylon, Australia, New Caledonia, Marianne Isles, Hawaii, West Indies and both coasts of South America, and the islands of South Trinidad and Galapagos. It appears to be quite absent from Peninsular India and the Malayan region. I can only suggest that this plant is sea-dispersed. It is possible that the small grains may be carried on the feet of birds, but, considering the way it appears to get to islands, it seems more likely that its grains or rhizome are floated.

Eragrostis tenella (*E. plumosa*).—This little grass, somewhat variable in form, is common as a weed of cultivation all over the warmer parts of the world, and is undoubtedly carried about by man, but there are forms of it which haunt sandy seashores, and Gardiner and Willis, in writing the "Flora of the Maldives," say it is one of the first grasses to reach a sand-bank, followed by *Scaevola*. It occurs in the Maldives and Minikoi, and the form there is var. *riparia*, which seems very close to the ordinary form on sea-sand in the Malay Peninsula, var. *viscosa*. Though this form has a very different habit from the *E. tenella* of cultivated ground, there are various connecting forms. The plant occurs in a good many distant islands, e.g., Cape Verdes, Christmas Island (where it was collected by Lister before any human being had settled there), Cocos-Keeling, Ile des Egrettes, Mauritius (on coral 10 feet above sea-level), Seychelles, Bourbon, Diego Garcia.

The small grains are free from the glumes, which can take no part in floating them, but Willis' and Gardiner's observations seem to show clearly that the seed will float, otherwise I should have suspected that it could only owe its distribution to drifting on floating timber.

Spartina.—These tidal-mud grasses are most abundant and numerous in species in America, chiefly in the northern part, and are certainly dispersed by sea, either in the form of the rhizome or the grain. *Spartina juncea*, of North America, growing both on swamps and in sandy beaches, has reached Bermuda. *S. braziliensis*, a plant found on the coasts of Brazil and Patagonia, is most closely allied to, and perhaps the original ancestor of, *S. arundinacea*, the Tussock Grass of Amsterdam Island, St. Paul's Island, Tristan d'Acunha, and all the surrounding islands, and Gough Island. There could be little doubt that the original Tussock Grass, from which *S. arundinacea* (an endemic species) is descended, reached these islands by sea, either its rhizomes or its seeds drifting

in the currents, though it is possible that adherence of the spikelets to sea-fowl played some part in this.

S. stricta and *S. alterniflora* are found on the South coasts of England in tidal rivers, as well as in Spain, Portugal, France, Holland, Belgium and Venice. These two closely-allied species have fairly long rhizomes, which, torn up by currents, can be drifted safely in the sea from place to place. H. S. Thomson, in a note on a specimen of *S. stricta* in Kew Herbarium, writes that he found several clumps on Berrow Flats, near Burnham-on-Sea, having probably been carried by the tide from the south of Clevedon, where it had been planted, a distance of 14 miles. F. W. Oliver (*Gardeners' Chronicle*, March 22nd, 1924, p. 161) describes a marshy swamp near Havre where, M. Duteutre says, formerly the strip of land at Hoc carried mainly *Salicornia herbacea*, then came *Aster tripolium*, then *Spartina Townsendii*, and later *Glyceria maritima*, each plant in turn supplanting the other. *Glyceria maritima* is a tufted saline grass of no great size, which is found on many parts of the coast of Britain and the Mediterranean region, and northwards to Iceland, the Faroe Islands, and Arctic America. I presume it is transported by sea along the coasts.

Spartina Townsendii is a plant with a remarkable history. It was first found at Hythe, near Southampton, in 1870, in 1889 at Southampton itself, and in 1893 it had reached Yarmouth in the Isle of Wight, and Cherbourg in France, 1905. It first appeared at Poole Harbour, Dorset, in 1907, where it is rapidly covering the mud flats and spreading widely. It seems to be mainly dispersed by portions of the rhizome or clumps of the plant.

Dr. Stapf (who gives a figure and account of it in *Bot. Mag.* t. 9125) found live rhizomes of the plant cast up on the shingle beach between Milford and Hurst Castle. It may also be disseminated by seed, the grain being rather large and more or less protected by the glume, but, as far as I could judge, in Poole Harbour it was spreading mainly by rhizomes. There can be little doubt that it is spreading by sea, and either rhizomes or grains must have been so carried to the Isle of Wight and the French coast. Up to the present time the plant has not been found in any other part of the world.

S. arundinacea, the Tussock Grass of Amsterdam and Paul Islands, Tristan d'Acunha and Gough Island, is a very different-looking plant, with a dense, close-set panicle of spikelets. It is allied to *S. ciliata* of Chile. The outer glumes of the small spikelets have a spiny keel, and though portions of the rhizome may be sea-dispersed, it possibly reached these islands by the adherence of its spikelets to the feathers of the sea-birds which nest in the tussocks.

Stenotaphrum is a widely-distributed genus of grasses with creeping stems and broad, flat, linear rachides with ovate spikelets in short racemes sunk in depressions of the rachis. A certain number of these grasses are usually found inland, and are undoubtedly carried about by man as fodder grasses, or distributed by cattle, but some are sea-sand plants which are clearly sea-dispersed. The little spikelets are provided with somewhat coriaceous glumes, by which they are doubtless floated in the sea. *S. secundatum* (*S. glabrum*) is very widely distributed, and constantly found on beach-sand. It is found in the South of France—but apparently only accidentally introduced—on all the coasts of Africa, St. Helena, South India, Ceylon, Maldives, Diego Garcia, Australia, Polynesia, North America, West Indies, Eastern South America, including Bermudas.

Stapf points out some minute differences between the Old and New World plants, but taking the plants as a whole (they being so closely allied), I group all this set together. *S. subulatum* occurs in Galega Island, Seychelles, Aldabra, Little Kei, Marianne and Cook Islands, Sophia Island (Ellice Group) (a remarkable distribution).

S. clavigera, a very distinct species with small spikelets, is peculiar to Assumption Island.

Allowing for the importation of these plants—at least, the common ones—occasionally as fodder grasses and accidentally in ballast, I think there is no doubt but that they are or have been mainly sea-transported. The Australian plant was first collected by Cunningham.

Lepturus repens is a slender tufted or creeping grass about 1 foot tall, with very slender jointed spikes 3 to 6 inches long, articulate and breaking up into joints bearing the small spikelets. It is found widely spread over the tropics of the Old World from East Africa to Polynesia, in sea-sand or on rocks, sometimes forming quite a mat or turf. It was abundant on cliff-edges in Christmas Isle. It ranges from Mombasa and Zanzibar to the Seychelles, Aldabra, Mauritius, Laccadives, Ceylon, Malay Peninsula (east coast), Cambodia, Malay Islands to the Philippines, including Christmas and Cocos Islands, Krakatau, Australia, Booby Island, Formosa and most of the Polynesian Islands, including Pitcairn. It appears to be quite absent from India. *L. tenuis* is an endemic species in Socotra. *L. cylindricus*, also a seashore plant, is common in Europe, and possibly has reached the Canaries by sea-transport, but it has also appeared in Australia, South Africa, and North America and Uruguay as a pasture grass, and is found in meadows and roadsides, doubtless introduced in grass seed, and *L. incurvatus*, a Mediterranean species, has appeared in England in ballast, but all these species or forms are doubtless sea-dispersed normally.

It is quite possible that the grains of some of the sea-sand grasses which are rather widely distributed, *Myriostachys*, *Elymus*, *Psamma*, and *Halopyrum*, have been sea-drifted, but it is doubtful whether they would stand sea-action. I have mentioned the first three under cases of drift by rhizome (*see* p. 254). *Halopyrum mucronatum* is a seashore grass with rather a large grain, oval and grooved on one side. It ranges from Arabia to Somaliland, and along the east coast of Africa, including Aden and Raya Island, and down the west coast of India from Scinde to Tuticorin and Ceylon. It thus appears to have migrated along the two coasts, but failed to get to any of the islands far from the shore.

GYMNOSPERMAE.

CYCADACEAE.

Cycas.—Most of the species of this genus are to be found on sea and river coasts. The seeds are borne on fan-shaped or linear-lanceolate sporophylls. They are ovoid, about 3 inches long, and float readily. According to Schimper, the buoyant tissue forms a layer inside the hard outer coat or testa of the seed. The seeds float for some months. The plant is also dispersed locally by bulbils, at least in the case of *C. Rumphii*, and, in the case of inland plants, sometimes seems to be exclusively reproduced in this way. *C. Rumphii* (often considered a variety of *C. circinalis*) is found not rarely in the Malay Peninsula in the middle of forests, far from any river or sea, often in dense woods at the foot of the limestone cliffs. The Malays, however, have a tradition that in the time of their ancestors they tied their boats up to these cliffs, which were then on the seashore. These inland *Cycas* seem always to reproduce by bulbils, which become detached and roll down the hills to some distance, and form fresh plants. I have only once seen flowers (female) on one of these forest *Cycas*. In Christmas Island is a *Cycas* which was very abundant when Andrews visited the island in 1897, but when I was there in 1904 I found it by no means common. It was reproducing by bulbils, and I saw no signs of its having ever fruited.

In open country, by large rivers or the sea, *C. Rumphii* frequently fruits. Being unisexual, it does not fruit unless there are male plants close by. Female plants half a mile or less away from a male, do not set fruit.

The genus is tropical and subtropical Asiatic. The commonly sea-dispersed form or species is *C. Rumphii*, a tree about 20 feet tall. It frequents seashores, in sandy or rocky spots, and is widely spread, but it is not rarely grown as an ornamental plant. It is found in Burma, Andamans and Nicobars, Maldives (dubiously wild in Ceylon), Malay Peninsula and islands, including Krakatau, Christmas Island, New Guinea, Australia and Polynesia, Japan, East Africa and Madagascar. I have included here several plants which are doubtfully identical, including the Christmas Island plant, which differs from typical *C. Rumphii* in its narrower pinnae, but of which the flowers and fruit are unknown, and *C. Thouarsi*, of the Mascarene Islands and East Africa. In Krakatau the tree found by Ernst in 1906 was 1 m. 65 cm. tall (5 feet 9 inches) and 80 cm. round. If the original seed was cast on the shore after the eruption in 1883, it would be only 23 years old. As these plants grow very slowly, this appears to be a very rapid growth for the time. Lhotsy states (" Vorlesungen über Descendenztheorie," pt. ii, 479) that an old *Cycas* found on Krakatau by Valeton in 1905 seemed to be the only remnant of the original vegetation. Ernst remarks that it is impossible to say if the plant he found was the identical one mentioned by Valeton, but that it certainly does not belong to the original vegetation, as it is growing on that part of the littoral zone which was formed by the eruption.

The different forms inhabit different areas. Thus *C. Rumphii* ranges from the Malay Peninsula to Australia and Solomon Islands. The chief Polynesian form is *Celebica*, which ranges to the Moluccas. The form *Thouarsi* is Mascarene and East African. It has spread some way into Central Africa from cultivation, but is probably indigenous on the coast. It is quite clear that the species as a whole is a sea-dispersed one ranging over the usual area of Asiatic sea-borne plants, viz., Polynesia to East Africa.

CHAPTER III

DISPERSAL BY ANIMALS

Foreword—Seeds Dispersed by passing through Animals—Dispersal of Seeds by Mammals, Lists.

Foreword.

Animals play a very important part in the dispersal of plants throughout the world, and chiefly in the following ways :

(1) By feeding on the fruits of the plants and passing the seed, not only unharmed, but actually more fit for germination. In a large number of cases the fruit or seed is especially adapted for this purpose, being developed into drupes or berries, or having a conspicuous eatable aril attached; but much dispersal of the small seeds of herbaceous plants is effected by the animals, mostly herbivorous mammals, eating the foliage of the plant, and with it swallowing the seeds, which are later evacuated unharmed.

(2) By the adhesion of fruits or seeds to their fur or feathers, these fruits or seeds being provided with hooks, bristles or spines, or with a viscous or gummy secretion which causes them to adhere.

(3) By the adhesion of the smaller seeds or fruits to the feet of an animal in mud in which the animal has been trampling.

(4) By the adhesion of portions of the plant, or even, in some cases, the whole plant or seedling to the fur or feathers of a bird, mammal, or reptile in such a condition that, on being dislodged at a distance, it may continue to grow.

Almost all groups of animals disseminate plants to some extent. The most important group, however, is that of the birds, on account of their abundance in all parts of the world, and of the very long distances to which they can fly, and their power thus of crossing long stretches of sea. There are few islands in which there do not occur plants whose seeds have been brought by birds. Mammals come next in importance, but (with the exception of fruit-bats, which, in the tropical and subtropical areas they frequent, transport seeds in the same way as do birds) their disseminative powers are confined to continents. They are important dispersal agents of herbaceous plants with small seeds, as they swallow these with the foliage of the plants they feed on, and are also the main disseminators of plants with adhesive fruits and seeds. Reptiles and batrachians, scantier and more limited in area and mostly insectivorous, add little to the dispersal of plants. It is possible that in the great Reptilian age, the secondary geological period, they may have been the disseminators of the *Gymnosperms* and allied plants of their era, but no evidence has been produced on that subject.

Fish disperse aquatic plants to a limited extent. Insects have much greater facilities for dissemination. The ants especially play a part of considerable importance in dispersing the seeds of herbaceous, and occasionally shrubby,

plants, though only for short distances, while *Diptera*, *Orthoptera*, *Homoptera* and some other groups freely spread spores of fungi, bacteria, etc., parasitic or non-parasitic, on plants and animals. Mollusca and Vermes occasionally disperse seeds and spores, and such effects as they produce are detailed in their place.

SEEDS DISPERSED BY PASSING THROUGH ANIMALS.

Seeds destined for being swallowed by animals are mainly those in a pulpy pericarp, being either drupaceous or baccate. Almost every order of flowering plants contains some of these animal-dispersed species, and in many orders all the species are baccate or drupaceous. In those destined for dispersal by birds, the fruits are almost always coloured, and of no very great size.

Besides these, we have fruits, usually 1-seeded, in which there is a coloured fleshy outgrowth known as the *aril*, which is the eatable part of the seed, and which in most cases cannot be detached by the birds or mammals which eat it, so that it has to swallow the seed as well as the eatable aril, and either regurgitate and eject the seed, or swallow it and pass it in the excreta.

Many dry seeds or fruits are dispersed by being swallowed, most commonly by herbivorous mammals, which, in browsing on herbaceous plants, swallow the small hard seeds with the foliage, the seeds passing undigested. Grasses, *Leguminosae*, *Scrophulariaceae*, and *Amarantaceae* are largely disseminated in this way.

In certain cases the germinating power of the dry seeds is, however, destroyed, chiefly in the case of finches and other granivorous birds, which crush the seeds they eat before swallowing them; geese and ducks, which swallow acorns and quite digest them; rodents, which nibble up seeds, and often ruminants, which, in regurgitating and re-masticating their food, make it very improbable that any seeds pass through the intestine unhurt. Collinge, however, has shown that even finches often pass seeds unharmed, and this happens, occasionally at least, in some of the other seed-destroyers mentioned above, but in the case of drupaceous fruits or berries, almost invariably the seeds pass through the intestines of the animal, not only unharmed, but much benefited by the treatment. Seeds so passed are known to germinate more quickly and produce stronger plants than those which have not been swallowed by bird or animal and acted on by the gastric or intestinal fluids.

Kerner states that in his experiments of feeding birds on various fruits, and sowing the seeds passed by them, he found that in the case of a blackbird, 75 per cent. of the seed evacuated germinated, in a thrush 85 per cent., in a rock-thrush 88 per cent., and in a robin 80 per cent. He says that the germination of the seeds which passed through a bird was usually (that is to say, in from 75 to 79 per cent. of the cases) tardy in comparison with the seeds germinated without passing through a bird or animal.

He notes, however, that in the case of a few berries, such as *Berberis*, *Ribes*, *Lonicera*, the period of germination was accelerated. This class of fruit being specially adapted for dispersal by birds in this way, this was to be expected. Kerner used very varied seeds and fruits in his experiments, and many (*Myosotis*, *Umbelliferae*, etc.) which are not naturally bird-dispersed, and though they might pass through the intestines unharmed, these would not necessarily benefit by a more rapid germination.

He states also that seeds of plants usually inhabiting well-manured soil, such as *Amarantus*, *Polygonum*, *Urtica*, after passing through the intestines of a bird, produced stronger seedlings than those which were cultivated without such preliminaries.

Phillips (in the paper on " Fruit Dispersal by the Pigeon, *Columba arquatrix*

in Knysna, South Africa ") found that the seeds of *Olea laurifolia*, *O. foveolata* and *O. capensis*, which normally took 12 months to germinate, did so in from 4 to 6 months after passing through the bird, and those of *Elaeodendron croceum*, which normally took from 12 to 30 months, after evacuation by the pigeon took from 6 to 9 months only, so that the digestive action of the intestines saves at least half of the period ordinarily required for germination.

H. Dingler (in " Der Verbreitung und Keimung der Rosen-fruchten," *Engler's Jahrbuch* 46, *Beibl.* 41, 1912) gives an account of some experiments with a blackbird to which he gave the fruits of *Rosa canina* var. *atrichostylis* and var. *dumalis*.

In the first experiment with var. *atrichostylis* he found that—

Of 12 stones taken from the excreta,	3	germinated ..	25 per cent.
,, 9 disgorged by the mouth,	5	,, ..	55 ,,
,, 91 not passed through the bird,	57	,, ..	62 ,,

In the second experiment with var. *dumalis*—

Of 6 evacuated, (in 3 days)	all	germinated	100 per cent.
,, 74 separated stones,	57	,, ...	77 ,,
,, 130 retained in fruit,	92	,, ...	70 ,,

The stones in the above experiment usually were passed in 2 or 3 hours.

These experiments do not thoroughly endorse the theory that the passing through a bird of the seeds necessarily improves the germinating powers, though in the second case the percentage of bird-dispersed seeds is much higher than those not even freed from the fruiting pulp. However, the experiments are perhaps too limited to base any general theory on.

Lyell (" Principles of Geology," chap. xxxvii) states, on the authority of Prof. J. S. Henslow, that the seeds of plants passing through the intestines of birds are deposited in a condition particularly suited for vegetation. " So " well are farmers in some parts of England aware of this fact that, when they " desire to raise a quickset hedge in the shortest possible time, they feed " turkeys with the haws of the common Whitethorn (*Crataegus oxyacantha*), " and then sow the stones which are ejected in their excrements, whereby they " gain an entire year in the growth of the plant." Ostenfeldt, in an experiment as to the germination of seeds of *Potamogeton* passed through the intestines of a bird, obtained a quantity of seeds of *Potamogeton natans* which had been swallowed and evacuated by a Swan (*Cycnus olor*). He found the seeds so passed germinated faster and better than those which had not been passed through a bird. The evacuated seeds consisted of the hard endocarp and embryo only. The other seeds he planted (the unswallowed ones) retained the fleshy exocarp. This, however, somewhat vitiates the experiment, for it is very probable—in fact, certain—that seeds freed entirely of exocarp germinate much faster than those which retain it, and which often refuse, except after a long period, to germinate at all. I noticed myself, in Singapore, that it was almost impossible to raise seedlings of many of the Wild Figs (*Ficus benjamina*, etc.), from seeds, though these plants came up everywhere in suitable spots where the seeds had been passed by birds or bats, nor did any seeds develop in the neighbourhood of the fig trees, however abundant the fruits were, except where it was obvious they had been bird- or bat-sown.

Mr. Raffill, the cultivator in Kew Gardens, informs me that the pulp surrounding the seeds acts as a preventative of germination in pulpy fruits, so that it is essential to remove it completely before planting, which the digestive apparatus of a bird would do effectually. Indeed, all gardeners clean the seeds of drupes or berries of any surrounding pulp before they plant them.

The American crow, as mentioned elsewhere, in feeding on the fruit of *Rhus*, swallows a quantity of sand and then water, and regurgitates the seed smooth, clean, and polished.

S. A. Ives (in *Bot. Gaz.*, lxxvi, 1923, 61) notes that the North American *Ilex opaca* is sparsely distributed in Nature, only one seed out of a million germinating. The pericarp is particularly unfavourable for germination. It is tough and woody, and only when it decays can the seed germinate. It requires a period of 2 years underground to germinate, and by that time the embryo is dead. The pulp of the pericarp is red and sweetish, and bird-eaten. This plant would evidently become extinct if birds were not tempted, by the colour and sweetness of the pericarp, to eat the drupes.

Kerner states that he made a large number of experiments, on mammals as well as birds, to test if the seeds passed through them would germinate. I have already quoted from his experiments on birds. The mammals he tested were the marmot, horse, ox, and pig. He fed the seeds to the animals and examined the excreta to see what seeds it contained; these were then laid on a bed of earth, and seeds of the same species which had not passed through animals were laid on a similar bed for comparison as to results. He found that almost all the seeds were destroyed at once or upon being chewed with the cud. A few millet seeds germinated from the ox dung, and one or two lentil seeds and oat fruits passed uninjured through the horse, while seeds of *Cornus alba*, *Hippophae rhamnoides*, *Ligustrum vulgare*, *Malva crispa*, *Raphanus sativa*, and *Robinia pseudacacia*, all germinated after passing through a pig, but the number of seeds which so germinated was small as compared with the fertile seeds swallowed, and the fruits and seeds of about 60 species had completely lost their germinating power.

The horse and ox crush their food so completely that it is not to be wondered at that many of the seeds are destroyed, and this would especially be expected in the case of oxen, which regurgitate their food and chew it again. Still, there can be no doubt that considerable numbers of seeds, especially when devoured with foliage, are disseminated by these animals, and horses, as is well known, pass so large a number of uninjured seeds, that the sparrows find it worth while to search for them, and one often find oats and other plants growing from the dung. Further details are given under the account of dispersal by mammals. Seeds so passed may be benefited by the remainder of the excreta acting as manure, as they are actually deposited in manured ground.

Phillips, in his account of the Knysna elephants, gives the period of germination of some seeds swallowed and passed by them, which I have mentioned under Dispersal of Seed by Elephants, on p. 357. He gives the germination periods of *Olea laurifolia* and 2 other species as normally 12 months; after passing through the Pigeon *Columba arquatrix*, they took from 4 to 6 months; after passing through the elephant, from 2 to 4 months. Of *Elaeodendron croceum* (normal from 12 to 30 months), after passing through the pig, from 6 to 9 months; after passing through the elephant, 2 to 4 months. The other seeds which he records, the germination period, after passing through the elephant, seem to be very short also. It thus appears that seeds are more benefited by passing through an animal than through a bird. This may be due to the greater amount of manure in the excreta of the mammal.

Sir D. Morris ("Dispersal of Seeds and Plants," *Nature*, xxxvii, 466) writes :—"It is a common occurrence in India to utilise the services of goats "to hasten the germination of *Acacia arabica*. The seeds will not germinate "in hot weather, and it is the regular habit, in order to save a season, for a "person desirous of a crop of seedlings, to bargain with a herdsman or neigh-"bour who possesses a flock of goats, to quarter them for some days in a small "enclosure, where they are fed on leaves and pods of the *Acacia*. The seeds

"passed, at once germinate." Dr. Watt says that several kinds of seeds are germinated in the same way. Several species of Guava (*Psidium guava*, etc.) do not easily germinate, but do so more readily if they are picked up from night-soil.

The inhabitants of St. Helena opposed Sir D. Morris's suggestion to use night-soil in manuring their crops, as they said it would cause the place to be overrun with *Opuntia indica*, the fruits of which are a favourite food of the people.

As I mention elsewhere, I have seen the stones of *Nephelium lappaceum* freely germinating from the excreta of the wild tribes of the Malay Peninsula, who swallowed the seed, pulp and all, entire. Stones of this fruit do not commonly germinate when merely sucked clean and thrown away.

It seems clear that, in spite of Kerner's experiment, seeds passed through mammals and birds do retain in many cases their vitality, and that, frequently at least, they are actually benefited by the action, in the case of drupes and berries, by the complete cleaning of the seed from the pulp surrounding them, and also, in the case of herbivorous mammals, by the excreta manuring the ground on which they fall. Even in cases of grain-eating birds, evidence is forthcoming that a considerable proportion of seed swallowed by the bird is passed uninjured and may germinate.

DISPERSAL OF SEEDS BY MAMMALS.

With the exception of the Fruit-Bats (*Pteropus*, etc.) (which can cross considerable stretches of sea, carrying with them and so disseminating seeds, almost as well as birds), the distance to which seeds can be borne by mammals is limited to continental areas, as they are not able to cross more than narrow arms of the sea. The tiger, pig, and rhinoceros can swim for 1½ to 2 miles, but that seems to be about their limit, so that seeds transported by mammals, exclusive of bats, are absent from oceanic islands.

However, as regards land areas they are often able to distribute plants very widely, and even if, as in the case of monkeys and rodents, they carry fruits but a short distance, the dispersal of the seeds away from the mother-plant is of no small value, and in lapse of time the species may be transported by these short stages to a long distance.

Owing to their hairy covering, mammals effect more in disseminating plants with adhesive fruits and seeds than birds do, as these fruits attach themselves much more readily to hair than to feathers, and the ungulates especially convey seeds and fruits in mud attached to their feet, often for long distances. Animals like the rhinoceros and elephant march many miles every night, and these rambling beasts may carry seeds attached to their feet, or in their viscera, over large tract of country.

In former days, from the Eocene to the Quaternary period, the mammals were vastly more abundant over Europe, temperate Asia and America than they are at the present day, as may be seen by the sketches of palaeolithic man in the caves of Altamira and elsewhere, of herds of horses, bison, wild ox, and elephants, and the great abundance of the bones of these animals found in the river-gravel deposits. The European lowlands must have swarmed with ungulates, great seed-dispersers, as Africa does in many parts to the present day.

These vast herds were partly destroyed by the spread of ice all over Europe in the Glacial period, and further reduced by hunting and agricultural man, who substituted for them herds of domesticated cattle, sheep and goats, which also have been responsible for the dispersal of many of the smaller plants, and by man carrying these animals into remote parts of the world, they have

brought with them as fodder, or attached to their hair or wool, many herbaceous plants now widely distributed, but formerly comparatively local.

Fruits destined to have their seeds disseminated by mammals are not brightly or conspicuously coloured. Showy fruits are destined for the attraction of birds, which, flying over or through the woods or plains, can readily detect them at a distance. Diurnal mammals could hardly see the coloured fruits among the thick foliage, and the colour would naturally be of no use to the nocturnal animals, civets, fruit-bats, etc. It is probable that these animals are directed mainly by scent. I have seen a bat (*Cynopterus*) at night fly straight to a green fig of *Ficus polysyce* and take it off without searching at all; and it is certain that civets and bats, working at night, somehow go straight to fruiting trees, disregarding all others. Conspicuously-coloured fruits *are* frequently eaten by mammals, when they come across them, but in all such cases the form and size of the fruit denote that it is for birds that they are destined, and not mammals. Occasionally we find fruits which are adapted for dispersal by wind or water which possess bright colouration, and are very conspicuous, such as those of many *Dipterocarps*—*D. pterygocalyx*, *D. oblongifolius*, etc., *Hopea* spp. and *Melanorrhoea Curtisii* and *M. Wallichii* with bright red wings, so conspicuous that I have been able to detect a fruiting *Melanorrhoea* in the woods 2 miles away. The ripe fruits of *Pteleocarpa* have bright yellow wings, the pods of *Parameria polyneura*, with its plumed seeds, too, have a bright red colouring, and the large poisonous sea-dispersed fruits of *Cerbera odollam* are often flushed with red. In all these cases the colouring is adventitious and of no advantage to the fruit. Indeed, it may possibly be injurious. I have seen nearly all the fruits of a tree of *Dipterocarpus cornutus* destroyed by monkeys, and those of *Parameria polyneura* torn to bits by them, and all the unripe seeds eaten up. *Dipterocarpus* fruits are, however, more or less protected by their resin, and those of *Melanorrhoea*, also resinous, are actually poisonous. Monkeys, squirrels and rats, however, when food is scarce, devour almost all fruit they come across. During a year of drought, when fruit was scarce, the squirrels gnawed into the fruits of *Calophyllum inophyllum*, in the Singapore Botanic Gardens, and destroyed the seeds. The fruit has a resinous outer coat, and is generally refused by all animals. The tree usually grows by seashores and is sea-dispersed.

A very large number of seeds are disseminated by the graminivorous mammals, chiefly ungulates, eating the herbage, and with it swallowing the ripe fruits, later passing the seeds. Such plants are mainly herbaceous ones grasses, etc., or low shrubs. This was doubtless a more important factor in the distribution of species in the days of the great mammal period, when the open plains and woods of the north temperate region and South America swarmed with these animals, as Central Africa does to-day.

Dispersal of Food-Seeds.—I here give an account of the food dispersal of seeds by mammals, either by their devouring the fruit and evacuating indigestible seeds, or by carrying off the fruit and rejecting the seed, and I also add the dispersal of nuts and acorns by rodents storing them in the ground or elsewhere, and failing to recover them.

I have added some account of fruits eaten by man and fertile seeds evacuated, but other cases of dispersal by human agency, and dispersal by adhesion to the fur of mammals, and to mud on their feet, etc., are to be found under the chapters dealing with those subjects.

Savages or wandering wild tribes of men may, like animals, distribute seeds of the fruits they have eaten by passing them in their excreta. In the temporary encampments of the Sakai tribes, who live in a wild state wandering about the forests of the Malay Peninsula, I have seen the stones of species of *Nephelium* (*N. lappaceum*, etc.), as well as the large seeds of the Durian (*Durio*

zibethinus), mixed with the excreta, having evidently been swallowed and passed by them The Malay, in eating the fruit, always swallows the small round stones of the Mata Kuching fruit (*Nephelium malaiense*), as the pulp is so thin and firmly attached to the stone that it cannot be removed except by digestion; yet this fruit is very popular with them, and trees spring up commonly in cultivated ground. They say it is the only healthy way to eat this class of fruits. A Chinaman in Singapore on one occasion died from a block in the intestines from a vast amount of the seeds of the Mangosteen (*Garcinia mangostana*), which he had been in the habit of swallowing with the pulp. Druce ("Flora of Oxfordshire") says that Tomato seeds pass through the intestinal canal and germinate, hence the appearance of the plants occasionally at a sewage outlet. P. C. Standley records that in Mexico the Indians eat the fruit of the Cactus (*Carnegia gigantea*) and later collect the evacuated seeds, as do the Californian Indians with the *Opuntia* fruits, and Johnston and Heusmann report also the dispersal in Africa of the seeds of *Opuntia decumana* by human agency in this way. The same thing happened also in St. Helena, and Morris states that the inhabitants of that island opposed the manuring of the ground with night-soil, as that would cause the country to be overrun with prickly pears from the evacuated seeds of the fruits on which the people had fed. Mr. Burtt (in his report on "Seed Dispersal by Animals in the District of Tanganyika in Africa") says "that, while at Matabele, it was noticeable to "what extent the local fruits played a part in the meals of the Turu native. "During his work at bush-cutting he was usually eating some fruit or other." Among these were *Grewia* (3 species), *Adansonia digitata*, *Tamarindus indicus*, *Borassus aethiopum*, and *Vitex Hillebrandii*. "In the instance of *Adansonia* and "*Tamarind* the seeds are usually expectorated, and *Borassus* seed, after the fruity "fibre has been removed, is thrown away, but in the case of the other species, "seed and tissue were swallowed, native faeces in the neighbourhood being "largely composed of *Grewia* seeds."

It is common to find fruit trees in forest where no one is living, but in many cases it is clear that there had formerly been a village, and the trees deliberately planted, though this is not always the case. I have seen isolated trees of *Nephelium lappaceum*, *Durio zibethinus*, and *Averrhoa carambola* scattered about where it is improbable that a village ever existed. I doubt if *Nephelium malaiense* and *Erioglossum edule*, the small astringent fruits of which are very favourite morsels with children, and perhaps *Flacourtia cataphracta*, are ever intentionally planted by natives. The fruit gathered is carried along by wandering tribes, and eaten by the way, or conveyed to the camping ground. In the first case the seeds are dropped, whether evacuated or expectorated, at different spots; in the second case, at a definite spot, where the family camp, and so eventually form an orchard or garden there. Sometimes the seeds are deliberately sown and the young plants protected, but it is much more usual, in the early stages of civilisation, to deposit the seeds anywhere about the camps or settlements.

Monkeys (*Quadrumana*).—Monkeys live mainly on fruits, although they also eat leaf-buds, insects, and birds' eggs. They haunt the big forests, usually travelling in small flocks or families, in search of food, and remain in the tops of the higher trees, rarely descending to the ground, and avoiding the open country if they can, for fear of terrestrial enemies, the tiger, leopard, and big snakes. Exceptions to this are the Baboons of Africa, and the Langur (*Semnopithecus* sp.) of India. The other species of this genus inhabiting the Malayan forests are strictly arboreal, and rarely, if ever, descend to the ground. The Langur, doubtless, like the Indian peacock, is a relic of the fauna of the forests formerly covering the Indian Peninsula, but now destroyed by cultivation, both the ape and bird having been protected by man for religious purposes.

When food is scarce, the monkeys will often descend to the ground in search of anything edible they can find, or to pass from one patch of forest to another, or to attack an isolated tree in fruit. They seldom travel to any great distance, however, but usually keep to one area as long as they can get sufficient food there. In the Malayan forests the *Semnopitheci* seem to me the widest travellers. Monkeys eat juicy or succulent fruits by preference, though they also eat pithy fruits, and occasionally chestnuts or acorns. Though many of the smaller monkeys can swim well, they rarely cross rivers of any size. The Anthropoid apes, such as the Mias (*Simia satyrus*), apparently never swim, and are quite unable to cross a river or even a large stream. They feed mainly on leaves and shoots, and eat but little fruit. The Gibbons (*Hylobates*) eat more, I think, than the larger apes, but most of the seed dispersal is effected by the small monkeys, *Macaci* and *Semnopitheci*.

In the Malay Peninsula the order was represented by 2 species of Gibbons, *Hylobates agilis* and *H. Lar*, the Macaques, *Macacus cynomolgus* and *M. nemestrinus*, and several species of *Semnopithecus*. The latter genus and the Gibbons usually lived in the mountain forests, at from 1,000 to 4,000 feet altitude, in the loftiest trees, while the Macaques inhabited the lowland forests which cover a large area of the Malay Peninsula.

Macacus cynomolgus, the K'rah, is the most common species of the Malayan monkeys, and as a number inhabited the jungle in the Singapore Gardens, I was able to observe their habits and food-plants. The fruits I have seen them usually devouring were those of various species of *Eugenia*, *Planchonia* and *Rhodamnia* (*Myrtaceae*), *Mangifera* (*Anacardiaceae*), *Calophyllum* and *Garcinia* (*Ternstroemiaceae*), *Dialium* (*Leguminosae*), *Elaeocarpus* (*Tiliaceae*), *Trichosanthes* (*Cucurbitaceae*), *Nephelium* (*Sapindaceae*), *Randia*, *Coffea*, *Gardenia* (*Rubiaceae*), *Willughbeia* (*Apocynaceae*), *Strychnos* (*Loganiaceae*), *Passiflora laurifolia* (*Passifloraceae*), *Artocarpus* (*Urticaceae*), *Aromadendron* (*Magnoliaceae*). All of these fruits (except the *Trichosanthes*, which has conspicuous scarlet fruits destined rather for dispersal by crows) are dull-coloured and not very showy, the reason for this being that colouring of fruits is of little use to monkeys, as, owing to their position in the dense foliage, they can only see short distances in front of them. The mass of leaves of trees and climbers prevents their seeing colours in the way that high-flying birds can, and, as I have pointed out, brilliancy of colour in fruits is useless to all fruit-eating mammals. Monkeys, however, eat any fruit they come across as they wander through the forest, coloured as well as uncoloured.

When the monkeys find a tree or liane in fruit, they attack it vigorously, tearing off branches and throwing about more fruit than they eat. They often bite off pieces of a fruit, then drop it and seize another one. As a rule, arboreal mammals do not eat the fruit as they gather it, but carry it off a little way, apparently to avoid being robbed by others, and if they drop a fruit they do not descend to pick it up again, but go on to another. Unless there is a scarcity, they do not eat unripe fruit.

It has been pointed out to me that *Willughbeia* seed requires to be thrown at the base of, or near, a large tree in order that the climber may have a support to climb on, and this is brought about in the following way: A monkey seizes a fine fruit to eat it, and his companions immediately rush at him to take it away. He scrambles off to the nearest big tree and, getting into the fork or behind a bough, devours it hurriedly for fear of being robbed, throwing the seeds to the comparatively bare ground at the foot of the tree, up which the young plant can eventually climb. The seedlings, on developing, commence by climbing up the bushes and low trees surrounding the bigger one, and, climbing ever higher, reach the top of the bigger trees, where they obtain full

sunlight, and eventually form immense masses of foliage, flowering and fruiting plentifully.

Such big fruits (often 6 inches long and 4 inches through) are too heavy for birds of any kind to carry off, and so depend on monkeys for their dispersal. But in sandy heath country in Pahang, ground covered merely by low bushes, where monkeys could not go on account of risks from the attacks of tigers, wild-cats, dogs or other enemies, I found a species of *Willughbeia* (*W. dulcis*) growing on a bush with smaller fruits, 3 inches long and 1½ inches through, of a conspicuous apricot-orange colour, and very sweet and juicy. This was evidently modified for dispersal by birds, for which its small size and bright colouring rendered it very suitable. When monkeys are abundant and fruit is scarce, especially in dry seasons, there is great competition among them, for monkeys rarely come down to the ground to drink water, but depend largely on dew and raindrops on the leaves, and the liquid contained in the fruit, at all events in forest regions.

Mr. A. D. Machado, when travelling in the Johor forests, saw a fight for a fruit tree between the monkeys, and described it to me: "Four or five "of the large long-tailed *Semnopithecus* had possession of a jungle tree in fruit "on the banks of the river, and a large number of the small *Macacus cynomolgus* "attacked them, and fought for the fruit-supply. The fight lasted for over "2 hours, and was not then finished. The small monkeys attacked from all "sides in detachments, and the *Semnopitheci* threw them into the river, often "falling in themselves as well."

In the case of 1-seeded drupes, *Eugenia*, *Calophyllum*, *Mangifera*, *Nephelium*, with seeds too large to swallow, they nibble off a portion of the succulent pericarp, or in *Nephelium* the aril, and throw the seed away. In many-seeded fruits like those of *Planchonia*, which resembles an apple, or *Willughbeia*, which is oval or pear-shaped, they tear the fruits to bits, or more often tear off a few portions, throwing away the fragments (which often contain seeds) in every direction, so that the ground is strewed with fragments of pericarp and seeds. The seeds of *Willughbeia* are quite soft, and usually purple and pink inside, and though they have no unpleasant taste and seem quite eatable, the monkeys will not bite them at all. In *Artocarpus rigida*, the Monkey Jack, the fruit is yellow and covered with short processes, the outside is readily torn to pieces, and the round firm seeds are enclosed in a sweet orange pulp, which is the part eaten. *Randia anisophylla*, *Gardenia* and *Strychnos ovalifolia* have a hard woody endocarp, which is bitten through, and the pulp surrounding the seeds eaten. The *Strychnos* is a peculiarly interesting fruit in this connection. The fruit is grey-green, quite round, and nearly as large as a tennis ball. The rind (endocarp) is hard but brittle, and contains a number of oblong seeds about 1 inch long, flattened, rounded at both ends, and silvery. These are enclosed in a greenish-black pulp of intense bitterness, and full, as is the whole plant, of brucine, a poisonous alkaloid allied to strychnine, and one of the substances used by the jungle tribes (Sakai) for poisoning their darts to kill monkeys, yet the K'rah (*Macacus cynomolgus*) eats a quantity of it, as do the Civet-cats (*Viverra*), swallowing the seeds and evacuating them later. I observed that, when the monkeys ate the fruit, they only took part of the bitter pulp, and threw away the rest of the fruit, for the broken fruits on the ground commonly contained a considerable portion of the pulp and some of the seeds. These broken fruits, however, allowed the escape of the seeds, and rain-wash would carry them away farther. As the fruit does not dehisce, I do not see how the seeds could be disseminated except for these animals. In the case of the civets, I often found the excreta on jungle paths, mainly consisting of a mass of half a dozen or more seeds, so that they certainly swallow the seeds in some quantity.

It seems rather remarkable that while these animals will devour readily this intensely bitter pulp, they refuse to eat the (to us) tasteless seeds of the *Willughbeia*, or Durian, or the rather pleasantly tasting seed of the Cacao (*Theobroma*), merely sucking off the surrounding pulp and throwing the soft seed away. In these soft-seeded fruits, *Willughbeia* and *Theobroma*, the seeds are not swallowed, though they are quite small, but merely thrown out.

In fruits with hard seeds, such as those of *Rhodamnia* and *Coffea*, the whole fruit is eaten and the seeds swallowed and evacuated.

In *Passiflora laurifolia* the egg-shaped fruit is bitten open, and the small hard seeds in their sweet pulp swallowed in the same way that human beings eat this fruit. In small drupes such as *Nephelium malaiense* and *Zizyphus calophyllus*, the hard round pea-shaped seeds are enclosed in a thin sweet pulp which is almost impossible to detach from the stone, so that animals eating these fruits must swallow the whole fruit. The soft fruit of *Garcinia* and *Baccaurea Motleyana* and *Lansium domesticum* contain from 3 to 5 soft seeds (according to species), the pulp is quite undetachable from the seed, so that it must be swallowed by these animals, for I have never seen any animal suck off the pulp and regurgitate the seed as human beings do with these fruits.

In the Pulasan (*Nephelium mutabile*) there are two forms, in one of which the flesh (aril), which is comparatively thick, adheres tightly to the stone, while in the other it is firmer and readily breaks away, being easily nibbled off. If a monkey ate the clingstone variety, the seed would slip down its throat, while from the freestone form it would bite off the flesh and throw the stone away. The clingstone variety would, by being swallowed, be more widely distributed than the freestone one. In drupes intended to be swallowed entire it is essential that the seed should not be too large for an animal to pass. There is, therefore, a decided advantage in the drupe being small and possessing a pulp which cannot be detached by nibbling.

Many large-sized and heavy fruits, like those of the wild Mangos, *Mangifera caesia* and *M. lagenifera*, are carried by the monkeys to a convenient perch to be eaten, and as they take some time to consume, the monkeys convey them usually to some little distance to avoid being robbed by their companions. In so doing they are frequently dropped only partially eaten, so that one often finds them at a considerable distance from the parent tree. The weight of such fruits has another advantage, in preventing them from lodging in the mass of climbers and thick foliage which often mats the upper part of the forest, so that they fall to the ground and may roll to some distance. In the case of the *Willughbeia*, big climbers which form a dense mass of foliage and branches on the tops of trees, the monkeys, as described before, gnaw the fruit to bits and throw away the seeds or portions of the fruit containing the seeds. If monkeys are scarce, the fruits are not broken up, and when ripe fall whole, in which case the seeds germinate in the decaying fruit, so that later one finds a small cluster of seedling plants where the fruit has fallen. After these have grown a few inches, however, all or nearly all perish from overcrowding, and in localities where monkeys are absent I have seen the ground covered with seedlings of which, in a few weeks, none have survived.

There are a number of species of the genus *Dialium* (*Leguminosae*) in the East Indies. They are trees of large size, with ovoid, black velvety pods, each containing a hard seed enclosed in a slightly acid but pleasantly tasted pithy substance. They are often collected by the natives for sale in the shops, and are highly popular. The monkeys are very fond of these, and one often sees the remains of the eaten fruit on the ground near a tree. The fruit is, unfortunately, relished by the monkeys before it is ripe, so that very often the whole crop is gathered green by them and so destroyed. Though, as a rule, animals will not eat unripe fruit, probably on account of its acidity or astringency,

in some cases apparently they do eat it, and so destroy for reproductive purposes the whole crop of a tree, but probably only when hard pressed for food, or because they temporarily require acid fruits. The fruits of *D. guineense* are stated by Buchwald to be eaten by the monkeys in Africa.

Spider-Monkeys (*Semnopithecus*).—The long-tailed Malayan Spider-Monkeys live largely on the fruits of the lofty trees of Malaya. They are very wasteful, throwing half-eaten fruits in all directions, and breaking off branches whenever they feed on a fruiting tree.

Koorders, in an article on *Sloanea javanica* (*Tiliaceae*), (Kgl. Akad. Wett. Amsterdam) gives an account of this tree, the seeds of which he says were dispersed by *Semnopithecus*. The tree is widely scattered in the Java woods, but I only knew of a single one in the Malay Peninsula. The fruit is woody and dehiscent, of a beautiful orange colour, the seeds are shiny black, almost enveloped in a fine orange-yellow aril. This aril is extraordinarily bitter, and the fruits he found on the ground were gnawed at, or near, the top of the aril. The large sweet-tasted embryo had only been eaten up in a few cases. Apparently the intensely bitter aril which surrounds the greater part of the seed protected it in most cases from the monkeys.

I do not think that the aril is intended to tempt the monkeys first and then deter them by its bitterness, so that they throw the seed away, as he seems to suggest. Animals soon learn which fruits are eatable and which are not, and if the monkey did not like the taste of the aril, it would leave the tree as soon as it had tasted the fruit. The intense bitterness of *Strychnos* does not deter the monkeys from the fruit—in part at least—though they often eat a portion of it, and not the whole fruit, as civet-cats do. It is more probable that they actually like the bitterness of the aril of *Sloanea* and the pulp of *Strychnos*, in moderation. There is also the possibility of their eating these bitter poisonous fruits medicinally. In keeping the local squirrels in captivity in the Singapore Menagerie, we found it necessary to put a betel-nut in the cage. These animals were very liable to attacks—often fatal—of Ascarides, but if an Areca nut was given to them, they would nibble it whenever they thought fit, and this prevented the injury from the internal parasites. The brilliant colouring of *Sloanea* fruit and its aril (which Miquel figures as bright red, both capsule and aril) certainly suggests that it is destined for dispersal by such birds as hornbills and pigeons, rather than by mammals. Birds undoubtedly eat the small poisonous yellow berries of various species of *Strychnos*, and are very partial to the little, black, intensely bitter drupes of *Brucea sumatrana*. It is clear, however, from Koorders' account of the *Sloanea*, that monkeys do disseminate the plants to some extent, even if occasionally they eat the embryo of the seeds.

The *Semnopitheci* also eat the fruits of *Strychnos nux-vomica* in India. Gamble (" Manual of Indian Timbers," p. 498) says : " The pulp of the fruit, though " containing some poison, is eaten by the Langur monkeys, *Semnopithecus* " *entellus* and *S. primus*. But while the Langur monkeys can apparently eat the " fruit, and even the seeds, without harm, other monkeys, as well as other " animals, and man, cannot do so, though it is said the Flying-Fox (*Pteropus*) " can do so with impunity."

This plant, unlike the Malay species of the genus, is not a climber, but a tree of moderate or large size. The fruit is a large orange-coloured, very conspicuous berry. The devouring of the fruit of other species of the genus by Malay monkeys (*Macacus*) has already been mentioned.

Troup (in the "Sylviculture of Indian Trees") states that monkeys (probably *Semnopitheci*) in India eat the fruits of Tamarind (*Tamarindus indicus*), of which they are instrumental in scattering the seeds, also the fruits of *Cassia fistula* (*Leguminosae*), *Terminalia belerica* (*Combretaceae*), of which the drupes are yellow

and succulent, and of *Cordia myxa*, with yellow viscous berries (*Verbenaceae*), and *Diospyros embryopteris* (*Ebenaceae*), *Aegle marmelos* (*Rutaceae*), *Spondias mangifera*, *Ficus bengalensis*, and *Artocarpus Lacoocha*.

Baboons (*Papio porcarius*).—Mr. Burtt-Davy tells me that in South Africa the Baboons (*Papio porcarius*) carry off the fruits of *Opuntia Tuna*, a Cactus, native of South America, but introduced and now widely spread over South Africa, and with the fruits carry bits of stem attached, to the rocks where they dwell. The discarded bits of stem grow and produce plants, and thus these animals disperse it. They also evacuate the seeds after eating the fruit. Johnston also says they distribute *Opuntia decumana* in this way. Phillips states that the baboons eat and disperse the fruits of *Ekebergia capensis* (*Meliaceae*) in Knysna, and *Curtisia faginea* (*Cornaceae*). R. Marloth ("Flora of South Africa," vol. iv) thus writes of *Hydnora Africana*, parasitic on the roots of *Euphorbias* :—"The fruit develops underground into a globular body, the "placentae being modified into a gelatinous starch-bearing mass in which the "tiny seeds are imbedded. Baboons, porcupines and jackals dig up the fruits, "and naturally carry the seeds to their haunts among the bushes, thus securing "the dissemination of the plant. The colonial name for it is Bavian-kost and "Jackal-kost."

Cynocephalus sp.—Monteiro (in "Angola and the River Congo," p. 194) writes :—"A large dog-faced monkey, *Cynocephalus* sp., is very abundant in "the rocky and arid littoral zone of Benguella. There are a number of trees "and bushes that yield them food in the shape of berries and fruit, especially "one called Umpegui (*Ximenia americana*), bearing plentifully an astringent "plum-like fruit." This plant belongs to the order *Olacaceae*, and is very widely distributed over the world. Being usually (outside of Africa) a seashore plant, it is largely sea-dispersed, but it is also known to be dispersed by pigeons.

Lewis (in the "Altitudinal Distribution of the Ceylon Flora") states that the fruits of *Trichosanthes integrifolia*, *Mangifera zeylanica*, *Canarium zeylanicum* and some of the red scitamineous fruits, are eaten by monkeys, and that he has found the seeds of *Caryota urens* in their excreta.

Beccari ("Nelle foresti di Borneo") states that the Long-Nosed Monkey, *Nasalis larvatus*, feeds largely on the fruits of *Sonneratia acida* (*Lythraceae*) a large-sized marine or tidal-swamp tree with green or brown fruit like a medlar in size and shape, pulpy, with several seeds, not too big for an ape to swallow.

Malays and Sakais also eat this fruit, which is, indeed, rather sweet and pleasant. It is probable, however, that the *Sonneratias* owe their main wide distribution to sea-transport.

Phillips says *Cercopithecus pygerythrus* eats the fruits of *Ekebergia capensis* (*Meliaceae*), and thus disperses it in Knysna, South Africa, and Bews says that the chief food of the Vervet (*Cercopithecus Lalandei*) is the gum and pods of *Acacias*.

Burtt records a species of *Colobus* feeding on the fruits of *Grewia platyclada* in Africa.

J. Buchwald (in "Der Verbreitungs-mittel der Leguminosen des Tropischer Africa," *Engler's Jahrbuch*, xix) says that the fleshy pods of some species of *Cassia*, etc., are eaten by 4-footed mammals, namely, Apes (in Africa), and mentions specially *Cassia tora*, *C. laevigata*, *C. sophora*, *C. goratensis* and *C. Sieberiana*, also *Tamarindus indicus*, *Tetrapleura Schweinfurthii*, *Prosopis biglobosa*, *P. africana*, *Tounatea madagascariensis* and *Dialium guineense*. He does not say what kind of apes he means, or whether he has actually seen them eating the pods. I have seen no monkeys eating *Cassia* pods or those of *Parkia*.

Lemurs (*Lemuroidea*) *Lemur catta*.—J. Sibree ("Naturalist in Madagascar," p. 243) says of this Lemur :—"Their winter food consists chiefly of the Prickly "Pear (*Opuntia*), while in summer they subsist chiefly on wild figs and bananas."

Nycticebus tardigradus, the Slow Loris, is also a fruit-eater in the Malay region. It eats largely of bananas and probably other fruits.

Bats (*Cheiroptera*).—Fruit-Bats occur all over the tropics. They feed exclusively on fruits, and in most cases search for them at night only. When there is a scarcity of fruits, they eat buds and leaves of trees. They are extremely abundant in tropical Asia and Australia, and species occur in Africa and South America. They are the most important and extensive seed-dispersers of any mammals, as they are very voracious, and can fly long distances. Species of *Pteropus*, Fox-Bats, have reached Cocos Island from Java, a distance of 700 miles, but were exhausted by their long flight, and perished on reaching the island. They are often to be seen a long way out at sea, and apparently can readily fly from Sumatra to the Malay Peninsula.

The Fox-Bats (*Pteropus*) range from the Mascarene Islands through India and Malaya to North and East Australia, the Liukiu Islands, and Formosa, and to Fiji, Samoa and other Polynesian Islands. These bats are the largest species in the order, measuring 4 or even 5 feet across the wings, and though they are by no means as swift on the wing as the smaller insectivorous bats, yet they contrive to make very extensive flights in a comparatively short time. They remain suspended to the branches of lofty trees all day, and start their flight in search of food at dusk, usually feeding all night, and returning to their roosting-place at dawn. If disturbed during the day, they will circle round in the sunlight, or even move off to some little distance. The Christmas Island Fox-Bat (*Pteropus natalis*) has a habit of flying about in full sun, as if to enjoy the light and heat, but I have never seen any of these bats seeking for food during the day. When breeding, the Fox-Bats collect in immense numbers in some part of a forest, often in a Mangrove swamp, and remain for some months, till the young are able to fly. In the Botanic Gardens in Singapore, on rare occasions—about once in 10 years—they used to come to breed in the Garden jungle, and it was calculated that between 70,000 and 80,000 at a time used to occupy the loftiest trees there. At dusk the greater number used to start in every direction in search of fruit, and could be seen flying for miles. Those with young seldom flew to any distance, but remained in the jungle, and ate the buds and leaves of the trees till they were almost leafless. Every evening, even after the colony had gone, these bats could be seen flying over, usually at great heights. I have often seen them a good long way out at sea, and from the fact that there is an endemic species on Christmas Island (*Pteropus natalis*), 240 miles from the nearest land, and that species is allied to, if not identical with, the one in Lombok, 1,000 miles away, and, furthermore, that a number of other species occur in remote islets, it may be concluded that they can fly very long distances. Blandford states that *Pteropus medius* can fly for vast distances, and Sternberg records his capture of one alive, though tired out, at sea 200 miles from land. According to Hodgson, *Roussetta amplexicaudata* can fly from 30 to 40 miles in a night, and, as I have mentioned, one species of *Pteropus* has on more than one occasion reached Cocos-Keeling Island, 700 miles from Java.

I have never seen these large Fox-Bats descend below 40 feet from the ground in search of food, and they feed on trees from 40 feet to 150 feet tall. Nor do they fly through dense forests, as the smaller *Cynopteri* often do, but as several species of *Pteropus* are recorded as attacking the bananas, and *Pteropus natalis* the equally short-stemmed Papaya, it is clear that in some cases they do come as low as 12 feet from the ground.

These bats seem to be especially fond of hard-fleshed, green drupes such as the fruits of *Sapotaceae*, *Symplocos*, *Eugenia*, *Calophyllum*, *Elaeocarpus*, *Mangifera*, *Livistona chinensis* and *Terminalia Catappa*. Most of these fruits have no method of inland dispersal except by rolling or bounding when fallen from a high tree,

and dispersal by mammals, such as bats, or, when they are fallen, by rats, or, in islands, by land-crabs.

Prain (in his account of the "Vegetation of Coco Island, Andamans") says that the Fruit-Bats carry off the fruits of *Terminalia Catappa*, bite pieces out of the fleshy side, and drop them far from the tree. The dispersal of these fruits is largely aided also by rats, which carry them off from the ground and eat the flesh of the drupe, and in Christmas Island the land-crabs did the same. Of course, in these large-stoned fruits, the bats do not swallow the stones, so that they cannot convey them from island to island, or very far away from the parent tree. They merely fly off with them, nibble away the flesh, and let the stones drop at some distance from the parent tree. However, in small-seeded fruits like figs, they undoubtedly swallow the seeds and pass them. Blandford, however, says that they do not swallow the seeds of the Guava and figs, but spit them out, only swallowing the pulp, as birds do with many fruits.

These bats, both large and small, feed most voraciously and rapidly when they find a tree in fruit, and come in large numbers to it. The *Pteropodes* fight furiously with each other for the spoils, making a great noise.

Pteropus edulis is the common species of the Malay Peninsula. It feeds on figs, especially those of *Ficus benjamina*, and fruits of *Nephelium* and *Xerospermum* (*Sapindaceae*), *Cyrtophyllum peregrinum* (*Loganiaceae*), *Terminalia Catappa*, *Calophyllum pulcherrimum*, and many other fruits.

Pteropus medius, of India, according to Blandford ("Fauna of British India"), is fond of most garden fruits except oranges, and also eats the fruit of the Neem Tree (*Melia Azederach*), Jamoon (*Eugenia Jambolana*), *Zizyphus* and various figs.

Pteropus giganteus, of India, eats the fruits of the Mahwa (*Bassia latifolia*), the figs of *Ficus religiosa*, *F. bengalensis* and *F. glomerata*, Guava, Bananas, and *Eugenia Jambos*. Troup says that Indian Fox-Bats eat also the fruits of *Anthocephalus cadamba*, *Diospyros melanoxylon*, *D. embryopteris* and *Calophyllum inophyllum*, and Cunningham (in "Some Indian Friends and Acquaintances") adds to these that they have a special liking for fruits of *Polyalthia*.

Pteropus Ariel, of the Maldive Islands, eats fruits of *Zizyphus*, *Terminalia Catappa*, *Calophyllum inophyllum*, and *Pandanus*.

Pt. conspicillatus, of New Guinea and Australia, is reported to feed largely on figs. *Pt. Geddei*, of New Caledonia, feeds on Breadfruit (*Artocarpus incisa*). *Pt. natalis*, of Christmas Island, according to Andrews, eats the fruit of *Carica Papaya*, of *Sideroxylon sundaicum* and of *Inocarpus edulis*. *Pt. seychellensis*, of the Seychelles, eats the large drupes of *Spondias cytherea*, and Mangos.

Cynopterus.—These are much smaller bats than the Fox-Bats, usually measuring about 6 inches across the wings. *C. Lucasii* and *C. marginatus* were the most common species in Singapore. During the day they hang up singly or in pairs beneath the Plantain trees or in similar shady spots. In limestone districts the *Cynopteri* frequent the caves in enormous numbers, whence they issue at dusk in small flocks at a time, probably to avoid the attacks of the Bat-Hawk. They search for fruit during most of the night, and are said to be extremely voracious. They feed from lower trees than the Fox-Bats do, and eat especially the fruits of *Adinandra* (*Ternstroemiaceae*), the figs of *Ficus benjamina*, *F. polysyce* and many other species, drupes or berries of *Eugenia*, *Elaeocarpus*, *Nephelium*, *Achras*, *Palaquium*, and other *Sapotaceae*, *Calophyllum*, *Cyrtophyllum fragrans*, Guava (*Psidium guava*), *Melia azederach*, *Livistona australis* and other Palms. They fly straight to the fruits and bite them from the tree, then carry them to a distance, usually from 20 to 50 yards away, and, suspending themselves from a bough, devour the flesh, drop the stones, and fly back to the tree for another.

On one occasion, when sleeping in a bungalow at Ayer Panas, in Malacca,

I was disturbed by a continuous fall of seeds, as large as bullets, on the floor, where they bounded and rolled about. This I found was due to the neighbourhood of a fruiting tree of *Elaeocarpus parvifolius*, which has globose green fruits 1 inch through. This tree was being raided by a number of *Cynopteri*. When they gathered the fruits they flew to the house and, hanging from a rafter in the roof, nibbled off the firm green flesh and dropped the hard bony seeds on the floor, on which by the morning there were dozens of these stones. These bats are so troublesome in eating the fruits of the cultivated *Nepheliums* that the natives have to protect the trees by enclosing the fruit in bags, or by tying the long whips of rattans armed with hooks to the branches, so that the bats get their wings entangled and torn by the hooks. They were extremely troublesome to our Gutta-percha trees (*Palaquium Gutta*). We found it practically impossible to protect the fruits, the seeds of which were required for planting, from these animals. As soon as they were ripe, or nearly so, the green one-seeded fruits were carried off, every one, by the bats, which took them away to some convenient tree 50 yards or more away, ate the green flesh, and threw down the seed. We employed an Indian bat-catcher to catch these bats with a clap-net, and he caught a large number; but before the night was over, the tree was cleared of the fruits, which they took so far away that we were unable to recover the seeds. From another tree the bats carried the fruits to a large *Attalea* Palm, about 100 yards away, where we recovered a number of the seeds. This Palm seemed to be a regular resort of the bats, for the ground beneath it was strewn also with the seeds of *Eugenia grandis*, brought from several hundred yards away.

Rumph ("Herbarium Amboinense") states that the fruits of *Nauclea elegans* (*Rubiaceae*) is eaten by the birds and bats, and the seeds scattered in the gardens of Amboina, where they develop into big trees. These fruits are really small fleshy heads of fruit with tiny seeds. He says, too, that the Bread-fruit (*Artocarpus incisa*) and Jackfruit (*A. integrifolia*) are eaten by bats and also birds of paradise, and of *Anona* (*Rollinia*) *mucosa* he writes that fruits are rarely left to ripen (on the tree), as bats and other night beasts do not let them, for as soon as they become red, fuscous, or blackish, the fruit and peduncle are carried off. Doubtless, though these animals do destroy much unripe fruit, they probably carry off some with ripe seeds at times. He also states that the fruits of *Mangifera indica* and *M. foetida*, two of the Mangoes, are eaten by bats.

The bats of the genus *Pteropus* and *Cynopterus* are absent from the mainland of Africa, though *Pteropus* is found in Madagascar and even on Pemba Island, but it never appears to reach the coast. These bats are replaced by other fruit-bats. *Roussettus Leachii*, of South Africa, feeds on Loquats (*Eriobotrya japonica*), R. *aegyptiacus* on dates (*Phoenix*), and R. *collaris*, of South Africa, disseminates *Olea laurifolia* and *Curtisina faginea* to some extent, according to Phillips. *Epomops*, another African fruit-bat, is reported to feed on figs and bananas. We have, however, but little information on the habits of the African fruit-bats.

There are a number of bats in South America and the West Indies which feed on fruits, either occasionally or always. Dobson (in the Catalogue of the *Cheiroptera*, British Museum) quotes Osburn (P.Z.S., 1865) as giving some notes on the food of these bats.

Phyllonycteris sezekorini, of the West Indies, feeds on the clammy cherry *Cordia collococca*. He observed that it simply ate the pulp from the skin, and it also ate of the breadfruit. *Artibeus perspicillatus*, of Mexico, the West Indies, and Brazil, ate the fruits of the bread-nut *Brosimum alicastrum*, *Cordia collococca*, and *Eugenia jambos*. *Stenoderma achradophilum* feeds on the fruits of *Achras sapota*, which it carried ¼ mile from the tree, and also ate *Eugenia Jambos* fruits.

Macrotus Waterhousei, of the West Indies, fed on the fruits of *Maclura tinctoria*, the Fustic tree, *Brosimum alicastrum* and *Eugenia jambos*. Osburn observed a number of spirts on a wall where these bats came, and these spirts of dried pulp contained fustic seeds.

Bates (in " Naturalist on the Amazons," chap. xii), writing of Bats on the Amazon River at Ega, says :—" I opened the stomachs of several of these " bats and found them to contain a mass of pulp and seeds of fruit mingled " with a few remains of insects. The natives say they devour ripe 'Cajus' " (*Anacardium occidentale*), and Guavas (*Psidium guava*) on trees in the gardens, " but, on comparing the seeds taken from their stomachs with those of all " cultivated trees of Ega, I found they were unlike any of them. It is there-" fore probable that they generally resort to the forests to feed, coming to " the village in the morning to sleep." He does not say of what species these bats were, but calls them Vampires. " It is the largest of all the South American " species, measuring 28 inches in expanse of wing. It had large leathery ears " and an erect spear-shaped appendage on the nose, and I found 2 species, " one blackish in colour, the other of a ruddy hue, and ascertained that both fed " on fruits." From Bates's description I take this bat to have been *Vampyrus spectrum*, a large bat which apparently always feeds on fruits, and is common in Brazil.

INSECTIVORA.

As their name denotes, the animals of this family, with at least one exception, feed exclusively on insects—worms and such animal food. The exception is the little Malay Tree-Shrew (*Tupaia ferruginea*) and possibly some other species of the genus abundant in tropical Asia. The Tupaia feeds largely on insects and frogs, but it is also a fruit-eater. In the Singapore Botanic Gardens it dug up seeds out of the seed-boxes and devoured them, and was caught in traps baited with coco-nut and bananas. In captivity it fed chiefly on bananas and pineapple. It used to attack the Cocoa-pods (*Theobroma cacao*) cultivated in the Gardens, and bite into the pods to get the sweet pulp surrounding the seeds, throwing the seeds about, as squirrels do. It also carried off and ate the hard green pericarp of *Alangium Ridleyi* (*Cornaceae*) and the arils of the sweet seed of *Dysoxylon cauliflorum* (*Meliaceae*), a tree which bears red capsules containing black seed with a red arillate mass at each end. These conspicuous fruits grow low down on the trunk of the tree, and are also fed on by squirrels and birds. The Tupaia lives chiefly on the ground, where it picks up these fruits fallen from the trees, though it will ascend trees to a height of about 10 feet, but rarely higher. It thus plays some part in dispersing jungle fruits.

CARNIVORA.

Felidae.—These animals, though certainly in the main carnivorous, eat fruit, and may thus disseminate the seeds to a small extent. The tiger is reputed in the Malay Peninsula to be very partial to Durians, and has been known to attack natives carrying baskets of them, and to carry off the fruit. In Pahang, on the Tahan River, a tiger remained one night round the camp, eating fallen wild mangoes. Spruce (in " Notes of a Naturalist," ii, p. 376) writes :—" It is well known how fond all animals are of the Alligator Pear " (*Persea gratissima*). I have seen cats prefer it to any other kind of food, and the " wild cat-like animals are said to be all passionately fond of it. I have been told " by an Indian that in the forests between the Uaupes and the Japura Rivers " he once came on four jaguars under a wild Alligator Pear tree, gnawing the " fallen fruits and snarling over them as so many cats might do." The fruits of the Alligator Pear are usually pear-shaped, dull green with a purplish flush,

and from 4 to 6 inches long. They contain a single globose seed. The fruits are too big probably for any American bird or bat to carry off, and it is quite possible that they are dispersed by terrestrial mammals only. Wild-cats are recorded (by Prof. Bray) as eating Juniper berries and passing the stones in the excreta, in North America (*see also under* Canidae, p. 353). Lewis says that in Ceylon the fruits of some of the red-fruited *Scitamineae* are probably eaten by wild cats, as he has frequently found cases to support this suspicion.

Bears (*Ursidae*).—The Brown Bear (*Ursus arctos*) feeds largely on the berries of *Vaccinium* and the fruits of *Rubi* in the northern regions of Europe and temperate Asia, before its winter sleep, and Nolte describes finding the seeds of *Rosa canina* in its excreta. It doubtless disseminates these plants to some extent. Heintz says it eats and disseminates fruits of *Rubus arcticus* and R. *Chamaemorus* and *Pyrus aucuparia*.

The Polar Bear (*U. maritimus*).—According to Simmons (in the " Survey of the Phytogeography of the Arctic American Archipelago "), the Polar Bear is reputed to be fond of the Arctic berries, and appearance of *Rubus Chamaemorus* in King William's Island may be due to this animal, though he admits that it may have been brought by the Esquimaux, who carry about the contents of the stomachs of Reindeer (a favourite food of theirs), which may have contained seeds of this fruit.

The Indian Bear (*Ursus torquatus*) is stated by Troup to eat the fruits of *Cassia fistula* (also eaten by Jackals), *Aegle marmelos*, the Bael fruit, and *Zizyphus Jujuba*, and to store up walnuts (*Juglans regia*), and he quotes Manson as saying that the fruit of *Phoebe attenuata* (*Laurineae*) is eaten by bears.

A. Henry states (in *Kew Bulletin*, 1926, p. 21) that in Burma Bears and Monkeys search eagerly for the fruit of *Taraktogenos Kurzii* (*Flacourtiaceae*), a fruit as big as an orange, containing numerous seeds in a pulp. The fruits fall to the ground and are devoured by these animals.

The American Bear (*Ursus americanus*) is said by C. A. Geyer to be very fond of the scarlet fruits of the Aroid *Lysichitum Kamschatkense*. The berries of this marsh plant are sunk in the fleshy rachis. It is a native of temperate Asia and North America. Mr. C. Eplin informs me that this Bear eats also the berries of *Vaccinium macrocarpum* and *V. ovalifolium*, and those of *Echinopanax horrida* (*Araliaceae*).

The Sloth Bear (*Melursus ursinus*), a native of South India and Ceylon, is largely dependent on fruit. R. S. Spittal (" Wild Ceylon," p. 62) says that in Ceylon it climbs the trees in search of the fruits of the Palu, *Mimusops hexandra* (*Sapotaceae*). The fruit is little over ½ inch long, and contains 1 or rarely 2 seeds. It is also largely eaten by natives. H. Storey (" Hunting and Shooting in Ceylon," 1921) adds that it feeds on the fruit of Mora (*Nephelium Longana*), Kon (*Schleichera trijuga*), Weera (*Elaeocarpus serratus*), Timbiri (*Diospyros Embryopteris*), Diwell (*Feronia elephantum*), and Damba (*Eugenia gardneri*). In these works only the native name of the fruits is given, but I have added in brackets the scientific name, from Trimen's " Flora of Ceylon."

The Malay Honey Bear (*Helarctos malayanus*) is a native of the Malay Peninsula and Borneo, and inhabits forests, where it lives on honeycombs and fruit, and can climb up trees after them. It is especially fond of Durians (*Durio zibethinus*,). The fruit is a round, leathery, green or brown capsule about 6 inches through, covered with short, sharp conic thorns. When ripe it splits into 4 or 5 lobes halfway down, exposing a number of pale, brown, firm, but not hard, seeds 1½ inches long, covered with a thick creamy arillate pulp. The fruit usually falls from the tree when ripe, and can be taken from the ground. The strong odour of the fruit is well known to everyone in the Malay region, and might well serve to attract the attention of any animal. The trees are very lofty, from 60 to 100 feet high, and the fruit is borne high

up on the thick branches of the stem. The bear can climb up to the fruit, but the tiger and such animals that cannot climb find the ripe fruit fallen to the ground. The outer spiny rind of the fruit is so tough that the bear has to use considerable force with its paw to pull the fruit open, so as to extract the seeds. The eatable Durian is not known to occur wild anywhere, but there can be no doubt that it was originally wild in the Malay region, where about 12 other species occur; while of the 4 other genera of which this section of the *Malvaceae* consists, 3 are Malayan and 1 Ceylonese. None of the other species of Durian are strongly scented, or as pleasantly tasting fruits as the *Durio zibethinus*.

D. testitudinarum, the fruits of which grow low down at the base of the trunk, is said to be dispersed by tortoises, and it is probable that *D. pinangianus*, in which the aril of the seed is conspicuously rose-pink, owes its dispersal mainly to large birds such as hornbills, which the native name "Durian burong" ("Bird's Durian") seems to confirm.

The large seeds are not apparently swallowed by mammals, although occasionally by wild men (Sakai), as I have mentioned elsewhere, but the pulp is eaten off and the seed thrown away. I gave a tame honey-bear a wild Durian (*Durio oblongus*). It tore the fruit to bits with its powerful claws, and ate the aril of the seed and a good deal of the placentas of the fruit, but would not eat the seed, spitting it out so that it fell some feet away. Another bear in the cage, seeing the seed fall, bit it, but apparently did not like the taste, and would not eat it. The aril of this wild Durian had no particular taste, so far as I could detect, though the bear seemed very eager to eat it, nor could I observe any unpleasant taste in the nut-like seed which it rejected.

The Bear Cat (*Arctictis binturong*) is also an extensive fruit-eater. Two wild ones in the Botanic Gardens, Singapore, constantly visited an *Achras sapota* bush or small tree, at a distance of several hundred yards from the jungle in which they lived, and ate the fruit as fast as it ripened, visiting the tree every night. A tame one ate fruits of the *Papaya* (*Carica papaya*), and the Rambai, *Baccaurea Motleyana* (*Euphorbiaceae*), and passed the soft seeds of the latter apparently quite unharmed.

The Badger (*Meles taxus*).—Nolte records finding the seeds of Vine (*Vitis vinifera*), *Prunus cerasus*, and *P. domestica* in Italy, in the excreta.

Civet-Cats (*Viverridae*).—The civets and their allies are among the most important seed-dispersers in the tropical forests of Asia and Africa. They are nocturnal animals possessing a great skill in climbing trees in the jungle. They live on small birds, but more largely on fruits, which they probably find by scent. The common Musang or Palm Civet of Malaya (*Viverra malaccensis*) was very abundant in Singapore, often living in the roofs of houses. It leaves its abode at dusk and wanders about in search of food most of the night. Some living in my house returned regularly at 9 o'clock to the nest, and went out later, returning again at sunrise. It is very destructive to cultivated fruits, and I have seen in the excreta the seeds of Coffee, *Gnetum sylvestre*, *Caryota Cumingii* (*Palmaceae*), *Limacia velutina*, *Mimusops elengi*, and *Strychnos ovalifolia*, and it also eats the fruits of *Artocarpus rigida* and *A. integrifolia*, the Jack, *Diospyros discolor*, *Achras sapota* and *Musa malaccensis*. It seems generally to prefer the sweet juicy fruits, and, as far as I know, does not eat figs, or the firm-fleshed drupes such as those of *Elaeocarpus*, which are popular with the smaller fruit-bats. In the days of Coffee cultivation this and other civets fed largely on the Coffee berries, and when Coffee estates extended round the Batu Caves in Selangor, I often saw in distant dark parts of the caves small groups of white etiolated seedlings of Coffee which had sprung up from the excreta of these animals, which retire to these dark shady spots in the daytime. The civets have the habit of voiding their excreta on bare spots, such

as jungle paths or open patches in the forests, places highly suitable for the seedlings, as giving them more light and a better chance of developing. The Coffee seeds so voided in open spots on the estate were at one time much valued by the planters, and boys were employed to collect them. They were known as Monkey Coffee or Green Coffee, and fetched a higher price in the market, as the animals, civets and monkeys, always selected the finest fruit to eat.

Besides the common Musang (*V. malaccensis*) we had also in the Malay Peninsula the large *Viverra zibethinus*, *V. tangalunga*, *Paguma leucomystax*, and several other species of *Viverridae*, all of which ate fruits largely, and disseminated the seeds, doubtless, in the same way.

In Hongkong Mr. S. T. Dunn tells me that he often found the stones of *Dracontomelum mangiferum* on rocks where they had been voided by civets. The seeds of this drupe are over 1 inch long, and very large to have been passed by the animals.

Civettictis civetta, the African Civet-cat, like the Malayan civets, is a great fruit-eater. It is of large size, about as big as a medium-sized dog. Mr. Burtt writes :—" Great quantities of seed were found in the faecal matter of this " animal," and the specimens of its excreta which he brought home confirm this, as they consist almost entirely of seeds. These masses of seeds included those of *Cassia goratensis* (a rather pulpy-podded species), *Ficus sycomorus*, *Balanites*, of *Grewia* several species, including *G. pachycalyx*, *Royena macrocalyx* (*Ebenaceae*), *Strychnos pungens* and *Vitex ixingensis*. He says: " In the " instance of the thicket *Grewia* (*G. Holstii*) the nearest bushes were " found to be over 200 yards from the situation in which the faeces " occurred, containing seeds of that species, i.e., in the sandy bed of the " Ugwandi River." The *Vitex* has a large plum-like fruit with an accrescent yellowish calyx.

Canidae.—The dogs, foxes, and especially the jackals, eat occasionally a certain amount of fruit, and undoubtedly disperse the seeds. Prof. Bray states that foxes, as well as raccoons and wild-cats, in Texas, eat large quantities of Juniper berries, and that the seeds often occur in their excreta (Phillips, " Dissemination of Juniper by Birds "). Nolte records finding in the excreta of foxes, in Italy, seed of *Prunus cerasus* and *P. domestica*, and of *Vitis vinifera*. (" The little foxes that spoil the grapes " are mentioned in the Bible, in the Song of Solomon.) Heinitz states that foxes in Sweden eat the fruits of *Vaccinium vitis-idea* and *V. oxycoccus*. A writer (in the Bulletin of the Plant Industry, U.S.A.: Plants Imported, no. 31, p. 44) says of *Lithraea caustica*, an *Anacardiaceous* shrub, native of Chile :—" The foxes are fond of this " fruit, and sow the same when cast away with their dung. Trappers look for " the dung containing the seeds, in order to set their traps." The plant is a bush allied to *Rhus*, with yellowish drupes as large as peas.

Jackals.—Schimper records that jackals disperse the seeds of *Citrullus*, presumably after biting up the fruits (Buxton, " Animal Life in the Deserts," p. 125), and Marloth describes the digging up and eating of the subterranean fruits of *Hydnora africana* by jackals as well as porcupines and baboons. The minute seeds of this parasitic plant may very well be regularly dispersed by these animals in South Africa. Jackals (*Canis aureus*) in India seem to eat a quantity of fruit. R. S. Troup (in " The Sylviculture of Indian Trees," p. 369) says of *Cassia fistula* that pods were laid down on the ground, and within a week the plot was discovered by jackals, who broke up the pods with their teeth to eat the pulp. Of the seeds thus treated by these animals, a large number germinated successfully, while of others, protected from these animals by wire netting, none germinated. The animals which naturally eat them are monkeys, jackals, bears, and pigs, and the seeds have been seen in their excreta. The tree

is a native of India, but it was very early dispersed by man to various colonies, as the fruit was highly valued in medicine. The pods are cylindric, 1 to 2 feet long and ¾ to 1 inch through, containing 25 to 100 flat seeds ¼ inch long, embedded in a sweet blackish pulp and separated by woody partitions from each other.

Jackals are also said by Troup to eat the fruits of *Lantana mixta*, probably *Aegle marmelos* (*see under Cervidae*, p. 371), *Zizyphus jujuba* and *Z. nummularia*, the stones appearing in their faeces, and the fruits of the White Mulberry (*Morus alba*) to some extent. Lewis says that in Ceylon he has seen the seeds of the Palm *Caryota urens* in their excreta. J. V. Phillips says that dogs in South Africa eat the fruits of *Olea laurifolia* and disseminate the plant.

Mustelidae.—These animals are mainly insectivorous or carnivorous, and do very little in seed-dispersal. However, St. John (in " Wild Sports and Natural History of the Highlands ") states that the Marten-Cat (*Mustela martes*) eats wild raspberries and blackberries.

The Skunk (*Mephitis*) lives mainly on animal food, like the badgers, but Dr. Avery records finding the seed of a Persimmon (*Diospyros*) in the rectum of a skunk in North America.

Cercoleptes caudivolvulus, the Kinkajou (*Procyonidae*) feeds largely on fruit, and Dampier notes that it was always in the Sapodilla trees (*Achras sapota*) in South America.

UNGULATA.

Elephants (*Proboscidea*).—The elephants feed largely on the shoots or leafy branches of trees, and in the East Indies on bamboo leaves when they can get them, but they also eat herbaceous plants, grasses and low herbs, and not rarely fallen jungle fruits. They wander very long distances, usually by night, and occur, or formerly occurred, over the whole north temperate area in both hemispheres, in Africa, and tropical Asia. They were remarkably abundant in Pleistocene times.

Elephas primigenius, the Mammoth.—The knowledge of the food-plants of this animal is derived from the contents of the mouths and stomachs of several specimens found preserved in ice and frozen ground in Arctic Siberia, where at one time they seem to have been extraordinarily numerous. They ranged in Pleistocene times from England, through Europe and Northern Asia, to North America. The fossil bones and tusks, as well as the palaeolithic drawings found in caves, show that they must have been one of the most common animals of the time, and rambled about in large herds. In the stomachs of the ice-preserved specimens have been found abundance of cones and branches of *Coniferae*, *Pinus*, *Larix* and *Abies*, but there were also found the remains of *Carex* and seeds of *Thymus serpyllum*, *Papaver alpinum*, *Ranunculus acris* var. *borealis*, *Beckmannia erucaeformis*, *Agropyrum cristatum*, *Hordeum violaceum* and *Oxytropis campestris* var. *sordida*, all species occurring in Siberia at the present day. (Sollas, " Ancient Hunters," Ed. iii, 215; Smith-Woodward, " New Mammoth at St. Petersburg," *Nature*, 1903, lxviii, 297; Bassett Digby, " Mammoth and Mammoth Hunting," p. 143.) Of the plants mentioned above, the seeds of probably all but the *Coniferae* could pass through the animal unhurt. The poppy *Papaver alpinum* and the Arctic form of *Oxytropis campestris* var. *sordida*, and the grass *Beckmannia erucaeformis*, are found in Arctic America as well as all over Arctic Europe and Asia. The *Beckmannia*, however, grows in Southern Europe as well, and has occurred (accidentally introduced) in Surrey and Middlesex. The Mammoth is recorded as occurring in Arctic America, and may perhaps have crossed the Behring Straits and carried these and other plants across. The *Thyme* and *Ranunculus* occur only in Greenland, and are not wild elsewhere in America. *Hordeum violaceum*

and *Agropyrum cristatum* do not occur in America or even as far as China or Japan; both are characteristic of Europe and temperate Asia. The Mammoth in Arctic Siberia seems to have fed on herbaceous plants during the summer and autumn, and on Conifers chiefly in winter, when the snow covered the herbaceous plants. In Pleistocene times it ranged from Ireland, through England and Europe, to the Mediterranean, across Siberia, and is probably responsible for the dispersal of many of the herbaceous plants over this area. At the same time it must be remembered that there were many other herbivorous mammals in great herds occupying the same area, the horse, bison, deer, and wild cattle, which doubtless played the same part as the Mammoth in distribution.

The Indian Elephant (*Elephas indicus*) chiefly frequents forests in the Malay Peninsula, and lives on branches of trees and bamboo leaves, but it also eats herbaceous plants. It is very fond of the tall grass *Themeda gigantea*, which grows in open country where the forest has been felled. It always beats a bunch of the grass against its fore-leg before eating it, in order to free it of unpalatable insects, and in this manner may scatter the seeds about as it walks along. These elephants frequently drop their dung on tracks which they make through the forest, as well as on open spots, and I have seen masses of it covered thickly with small herbaceous seedlings of some plants too young to identify. Some of these tracks, where damp enough, are covered with a turf of *Isachne* or other low grass, and small *Cyperaceae*, *Fimbristylis*, etc., and other plants perhaps brought by wandering animals who use these tracks. The elephant rambles to great distances through the forests. In Ceylon R. L. Spittal (" Wild Life in Ceylon ") states that the elephants eat the fruit of the Palu (*Mimusops hexandra*), a tall sapotaceous tree with drupes containing one hard seed, as also do wild pigs and deer. The fruit is usually gathered from the ground after it has fallen. Troup says that wild elephants in India eat the fruits of *Dillenia indica* (*Dilleniaceae*), and are a possible cause of the dispersal of this tree; however, as far as I have seen in the Malay Peninsula, the seeds are usually dispersed by streams, on the banks of which it grows. The sepals in this fruit, after the fall of the petals, close over the carpels, and become very thick and fleshy, the whole fruit then being more or less globose, and about 6 inches through. The numerous seeds in the carpels are very small.

Van Leeuwen quotes Rutgers as having seen germinating seeds of some species of *Mangifera*, and Westeneuk as seeing germinating rice (*Oryza sativa*) in the dung of elephants in Sumatra.

The African Elephant (*Elephas Africanus*).—Mr. B. D. Burtt, while living in Matabele, Singida district, Tanganyika, had many opportunities of observing the behaviour of the wild elephants in that part of Africa, and to him I am indebted for an account of the habits of these, and other animals of that area. He says: " The abundance of seeds in the dung of elephants suggested that, " by the wandering of these animals from one feeding ground to another, " the dispersal of certain species of plants from the parent community was " considerable." He gives in a report, from which I take these notes, a list of the species of plants whose seeds were found in the dung of the elephant, as follows:—*Acacia spirocarpa*, *Adansonia digitata*, *Balanites aegyptiaca* and another apparently unknown species, *Tamarindus indicus*, *Strychnos pungens*, *Sclerocarya Birrea*, several species of *Grewia*, *G. platyclada*, *G. mollis*, *G. Holstii*, *G. bicolor*, *G. pachycalyx*, *G. flavescens*, *G. corylifolia*, and *Borassus aethiopum*.

Elephants feeding along the Ugwandi and Twumbu Rivers showed great preference for the fruit of the *Borassus*, as their dung frequently contained seeds of this Palm. In many instances a single seed was found in the stool, while one stool revealed 9 individual seeds. On three occasions the seeds were found to be germinating, the radicle having taken firm root in the soil

below. Many clean seeds were found beneath the Palm trees, having evidently had all the fibre and fruity tissue removed, and had then been expectorated. Some seeds which had passed through the animal were brought home by him and measured—(1) 5¼ inches long, 4¼ inches wide, and 3½ inches thick; (2) 5¾ inches long, 5 inches wide, and 2 inches thick. They are covered, when fresh, with pulp and fibre. That seeds of this size can be passed by these animals is very remarkable. David Livingstone (in his " Missionary Travels," 1857) says also that the elephant shakes the Palmyra Palm (*Borassus*) for the fruits, which it picks up and eats, and this is confirmed by D. D. Garnett (in *Country Life*, October 21st, 1927, p. 446), who, writing of the Semliki plains in Uganda, says that the elephants are passionately fond of the fruit of the *Borassus* Palm, and their tracks are often to be seen converging to an isolated tree, around whose base the ground is trodden down hard, and littered with the fibrous kernels of the fruit which had been rejected. It is undoubtedly due to the seeds transported in the viscera of the elephant that the Palm owes its spread. *Borassus aethiopum* occurs all over Africa, and a species much resembling it in India, whence it has been carried to the Malay Peninsula, Cambodia, and the Malay Islands by natives. There is also an allied species, *B. machadonis*, a forest tree, very local in the Malay Peninsula. Elephants are found all over the area occupied by *Borassus*, except in a few places where the Palm, sacred to the Hindus, has been transported by man, who must therefore also be associated with the dispersal of it.

Elephants have a great fondness for the pods of *Acacia spirocarpa*, as their dung usually contains the seeds of this species in considerable quantity. The fruits of this plant are also popular with giraffe, eland, impalla antelope, and domestic cattle. The pod is rather thick, and coiled (*see under* Cattle, p. 365). Seeds of *Adansonia digitata*, *Balanites* and *Tamarindus indicus* were found only very rarely, a surprising fact, as these species abound in the neighbourhood of the rivers and are heavily loaded with fruit. *Adansonia* (*Malvaceae*), the Monkey Bread, is popular with eland and also with natives. Burtt-Davy tells me that the fruits of *Balanites tomentosa* and *B. aegyptiaca* are a favourite elephant food in Portuguese East Africa, and that the stone of this drupaceous fruit is hard and indigestible, and is said to pass through the alimentary canal undigested.

" In several instances the fruits of *Sclerocarya Birrea* (*Anacardiaceae*) were " found in elephant dung. On one occasion the fruit had passed through the " animal, the softer tissues having been scarcely corroded by the digestive " juices." The fruit is a sweet pulpy drupe, like that of *Dracontomelum*. The species above-mentioned appears to be undescribed. There are 2 or 3 species of the genus, which is peculiar to Africa.

" Seeds of 3 species of *Grewia* abounded in the dung of elephants. All " stools yielded seed in great quantity. Some showed almost pure stools of " the thicket *Grewia* (*G. Holstii*). Those found along the river contained almost " pure seeds of the 'riverine' *Grewia* (*G. pachycalyx*). One large stool " investigated near the Nugamba Pool showed that the riverine *Grewia* seed " had been carried some 10 miles from the nearest considerable locality for " this species. Leaves of *Tamarindus indicus* and *Hippocratea obtusifolia*, that " occur nearest at the Twumbu River, confirm this."

One of the faecal pellets of the elephant, brought home by Mr. Burtt, contained hundreds of *Grewia* seeds and very little else. Five species of *Grewia* were found in the excreta, two which form thickets, *G. Holstii* and *G. platyclada*, and one which frequents the river banks, *G. pachycalyx*. As the excreta, dropped by the elephants when drinking at the river bank, float for some time, the seeds may readily be carried away by the water to some distance. The *Grewias* are mostly shrubs or small trees, and the elephants, seizing the boughs, which are loaded with the small drupes, strip the fruits off in their mouths, much as children eat.

currants. There is a little sweetish or acid pulp on the fruits, sufficient to make them popular with the natives. The fruits are dull-coloured; *G. corylifolia* brown, with sweet pulp, *G. mollis* and *G. bicolor* dull yellowish, with hard pulp. The *Grewias* are widely-spread shrubs or small trees found all over Africa and Asia. The fruits are usually firm-fleshed and dull-coloured in Asia, and dispersed by fruit-bats, but a few have pulpy orange or red fruits.

Strychnos pungens.—The fruit of this bitter plant is also eaten by these animals, as well as by the eland and other animals, according to Mr. Burtt.

Grant (in "Speke's and Grant's Travels") says of *Acacia Seyal*:—"Elephants are very destructive of these trees, for they knock them down to "get at the fruit." David Livingstone (in his "Missionary Travels," 1857) says that the elephant eats the fruit of the "Masuka and Makarongo," and other fruit trees. The latter fruit he describes as a black-coloured plum, but I have not been able to identify either of these plants. In chap. viii he mentions finding grape vines of which the fruits were eaten by bushmen and also by elephants, which are fond of the fruit, plant, and root alike. In Kew Gardens Museum there is a specimen of the seed of a Palm, *Hyphaene* sp., found in elephant dung on the Zambesi. The seed is 3 inches long and nearly as much through. The elephant is said to haunt regularly the groves of this Palm, and Kirk states that they feed largely on the fruits of *H. crinita*.

Mr. Burtt-Davy writes to me that "*Treculia Africana* (*Moraceae*) furnishes "in its fruits (from 18 to 30 lbs. in weight) a favourite fruit of the elephant. "The fruits are said to contain up to 15,000 seeds." I had trees of this plant in cultivation in Singapore Gardens, which bore oblong-globose compound fruits after the style of a Breadfruit, but by no means as large as those described by Mr. Burtt-Davy, perhaps from the locality being unsuitable, or the trees too young. The heads of fruits were green and possessed a pleasant scent, but were rather woody, like the fruit-heads of the allied *Artocarpi*, which, however, are soft and juicy. They fell entire when ripe. The fruit-heads of the Jack, Champedak, etc. (*Artocarpus*) are commonly bitten to pieces on the trees by monkeys and squirrels, who carry off the seeds.

Mr. J. F. Phillips (in the "Knysna Elephants: their History and Habits," *Report of South African Assoc.*, xxii, 207) gives a list of the food-plants of the elephant in South Africa, which he says eats the foliage of various plants, swallowing also the seeds, which germinate well after passing through the animal: *Solanum giganteum*, *S. nigrum*, *S. aculeastrum*, *S. tomentosum* (these plants have small, flattened, tough seeds, many thousands of which occur in each faecal roll; these germinate in from 7 to 20 days), *Physalis pubescens*, *Gnidia* spp. (seeds passed germinate in 7 days), *Struthiola* spp., *Psoralea* sp. (seeds germinate in 14 days), *Ficus lutea* (seeds germinate in 30 days), *Scutia indica* (within 2 months), *Acacia melanoxylon* and *A. decurrens* (from 7 to 21 days), *Virgilia capensis*, *Elaeodendron croceum*, *E. capense*, *Olea laurifolia*, *O. capensis* and *O. foveolata* (germination of these 5 plants takes place in from 2 to 4 months), *Myrsine melanophlaea* (from 1 to 2 months), *Podocarpus elongata* (from 4 to 8 months).

The dispersal of many of the smaller herbaceous plants, as well as the low bushes, over the African plains must be due to the elephants, as well as to the other browsing animals.

Rhinoceros.—These animals feed on low herbaceous vegetation, leaves of trees, and on fallen jungle fruit. I have comparatively little information as to the part they play in seed dispersal, but it is probable that they are of some importance.

Prof. Brandt, in a letter to Alexander von Humboldt (*Quart. Journ. Geol. Soc. Lond.*, iv, p. 10; Lyell's "Geology," chap. vi), states that he has extracted from the cavities in the molar teeth of the extinct European *Rhino-*

ceros tichorhinus fragments of pine leaves and portions of the wood, and half of a Polygonaceous seed, so that, though this animal chiefly ate pine boughs, it also browsed on herbaceous plants and doubtless distributed the seeds.

In the Kew Gardens Museum are two seeds taken from the caeca of *Rhinoceros sumatrensis* which died in the Zoological Gardens, Regent's Park. The seeds are those of *Entada Schefferi* and *Mezzettia leptopoda*, both seeds in good condition. The tickets on them stated that they were both sent by Prof. Garrod in 1877, and that the animals came from Chittagong and Pegu respectively. Major Flower kindly looked up the Zoological Society records, and found that only two specimens of the animal were received about that date, one in 1872, which died a month later, and was dissected by Garrod, and one received in 1875, date of death unknown. Both of these animals were bought from Jamrach. The first came from Sungei Ujong, the second said to be from Johor, both in the Malay Peninsula. The fruit of *Entada* is a large, rather hard pod containing a number of these large seeds (*see* p. 284). That of *Mezzettia* (*Anonaceae*) is a large 2-seeded, green, rather fleshy drupe. The seeds are extremely hard, and about 1½ inches long. The tree is a gigantic one, over 100 feet tall, and the rhinoceros must have eaten the fallen fruit and passed most of the seeds, one having remained in the caecum. *Mezzettia leptopoda* is only known from the forests of the south of the Malay Peninsula.

It is clear from these specimens that these animals eat fruits fallen from the big trees in the forests, and swallow the seeds, of which they probably pass the greater number uninjured. How long they are able to retain these hard seeds in the caecum unharmed, should they accidentally become enclosed in it, it is not easy to say, but it must have been some months at least in this case.

Rhinoceros sumatrensis is an animal that often wanders to great distances. It frequently has a regular route for very many miles, which it constantly travels, a march occupying it a month or more. It generally, like the tapir and other ungulates, evacuates only at special spots, frequently a long way from where it has been feeding, and consequently may carry and distribute seeds at long distances apart. It is probable that many others of the larger beasts of the jungle aid in the same way in dispersing the fallen fruits from the gigantic forest trees, of which so many are often to be seen bestrewing the ground in the mountain forests, and which seem otherwise to have no means of dispersal except by falling, and in some cases rolling a short distance, and by rain-wash. The Wild Ox (*Bos gaurus*) and the tiger eat fallen fruits, as well as the rhinoceros.

The Indian Rhinoceros (R. *unicornis*) is stated by Troup to eat the fruits of *Melocanna bambusoides*.

Rhinoceros bicornis, the African Rhinoceros.—Mr. Burtt, examining the excreta of this animal, found it chiefly composed of small wood chips. The only seed found in it was that of *Acacia verugera*, in considerable quantity.

Pigs (*Suidae*).—The jungle pigs (*Sus*, *Dicotyles*, etc.) certainly devour a good deal of fallen fruits, but I have comparatively few records of observations. Troup says that the Indian Wild Boar (*Sus indicus*) feeds on the fruits of *Terminalia belerica* (*Anacardiaceae*) and the pods of *Cassia fistula*, also *Aegle marmelos*, *Zizyphus jujuba*, and *Spondias mangifera*.

The domesticated pig, which has run wild in many parts of the globe, feeds also on fallen fruits. Amadeo (*Nature*, xxxvii, 535) says that in Porto Rico the Sour Sop (*Anona muricata*), the Sweet Sop (*A. reticulata*) and *Carica Papaya* are believed to be dispersed by hogs, as well as by horses and other mammals, and birds.

Sir Hans Sloane recorded that in Jamaica wild swine fed on the fruits of *Mammea americana*. Guppy says that in the West Indies, also, they eat the fruits of the Hog-plum (*Spondias lutea*) and *Anona palustris*. Hall says that in Hawaii

the tame pigs distributed the seeds of *Prosopis juliflora*, and the very large fruits of *Stemonurus megacarpus* of the Solomon Islands, the seed of which is 3 inches long and 2 inches in diameter, and is said to be sought by pigs, which eat off the cuticle and outer flesh. In South America Johnston says that the seeds of *Opuntia decumana* are dispersed by pigs.

The herds of tame pigs, formerly kept at pasturage in the woods in England, are said to have been responsible for the dissemination of Oaks, as in feeding on the acorns they frequently trod them into the soil, so that they germinated successfully, and the comparative scarcity of Oak seedlings in our woods at the present time, and the slow reproduction of the tree, are said to be due to the abolition of these herds of swine.

Heintz states that pigs feed on, and disperse the seeds of, *Rumex acetosella*, *Chenopodium album*, and *Stellaria media*.

W. I. Francis (in *Queensland Agric. Journ.*, 1920, p. 70) writes of the native Tamarind (*Diploglottis Cunninghami*) (*Sapindaceae*): "The ripe " fruits, which are very acid, are greedily eaten by pigs, which will often travel " some distance for them, and daily revisit the trees for the fruit as they ripen " and fall to the ground."

Phillips states that, like many other animals, they feed in South Africa on the fallen fruits of *Olea laurifolia*.

All the pigs seem to bite up their food very much, and largely destroy the seeds, so that they are rather poor disseminators, but Phillips says of *Potamochaerus*: " If there is much food, and the animal eats voraciously, many " seeds pass unharmed."

Potamochaerus chaeropotamus, the Wild Pig of South Africa.—J. F. V. Phillips gives an account of the habits and food of the wild pig (in the *Report of the African Association*, xxiii, 1926, p. 655). He says it eats fruits largely and destroys the seeds of many, but some seeds of the following plants pass through its viscera unharmed—*Podocarpus elongata* and *P. Thunbergii* some escape destruction), *Olea laurifolia*, *O. capensis*, *O. foveolata*, *Curtisia faginea*, some pass safely, as do those of *Olinia cymosa*, *Plectronia Mundtii*, *P. ventosa*, *P. obovata*, *Rhoicissus capensis*, *Ficus capensis* (some), *Virgilia capensis*, *Myrsine melanophlaca*, *Sideroxylon inerme*, *Apodytes dimidiata*, *Ilex mitis*, *Rhamnus prinoides*, *Gardenia Rothmanniana*, *Halleria lucida*, *Elaeodendron croceum* and *E. capense*.

Dicotyles sp.—Standley (in the " Flora of the Panama Zone ") says that peccaries are very fond of the fallen pods of *Prioria copaifera* (*Leguminosae*).

Camels (*Tylopoda*, *Camelus dromedarius*).—Aitchison, in his account of the " Botany of the Afghan Delimitation Commission " (*Trans. Linn. Soc.*, ser. ii, vol. iii, p. 4) writes that :—" At Zaru (Afghanistan) were some large " bushes of *Lycium barbarum*, almost devoid of foliage, but covered with bright ' red fruit like small capsicums. Here we lost several camels, from no known ' cause, though all those found dead were lying near these bushes, and had ' been eating greedily of the berries. I opened several camels, but the post- ' mortem showed no symptoms of irritant poisoning, yet there was nothing ' I could detect in their paunches except the berries. The natives said that ' the *Lycium* was not poisonous, and subsequently I often saw camels browsing ' on this shrub without any ultimate evil effects."

M. Boullu (*Bull. Soc. Lyon*, 1888, p. 58) says that the natives of Morocco feed their camels and goats on the fruits of *Argania sideroxylon* (*Sapotaceae*), and collect the seeds passed by these animals for making oil, and no doubt the plant is often dispersed in this way. H. C. Hart (in " Fauna and Flora of Sinai and Petra," 1891) mentions *Nitraria tridentata* (*Zygophyllaceae*), with small orange berries, as eaten greedily by camels. The pods of *Prosopis spicigera*, a favourite food with goats and cattle, are also eaten by camels in India.

Horses (*Equidae*, *Equus caballus*).—The horse, a greedy feeder, swallow,

and passes seeds of herbaceous plants very largely, much as cattle do, but as it does not chew the cud, probably a larger percentage of seeds pass through the viscera unharmed. Indeed, the sparrows know this well, and hasten to search the droppings as speedily as they can for uninjured seed. Horses, however, are not so widely dispersed as cattle, nor are they often allowed to roam widely over great areas, nor are they driven from place to place in large herds, as is the case with horned cattle, except in a few parts of the world. In Palaeolithic times (Quaternary epoch) wild horses were very abundant all over Europe, and even at the present time there are large numbers of wild (feral) horses in South America. *Prosopis juliflora* and *Euphorbia Drummondi* have already been mentioned as disseminated by horses, though, according to Prior, the former is said to be injurious to them. Ewart says that *Cyperus rotundus* is dispersed by horses, and I have seen the following plants springing up directly from their dung—*Bromus sterilis*, *Avena sativa*, *Cerastium triviale*, *Cicer arietinum*, *Vicia sativa*, *Stellaria media*, and in Christmas Island *Amaranthus viridis*, *Ageratum conyzoides* and some other weeds were disseminated by them.

J. Adams (in " Vitality of Seeds Passed Through Animals ") records that from horse dung he was using to grow certain fungi on, came up, besides oat plants, *Lolium perenne*, *Bromus mollis* and *Holcus lanatus*. Horses do not, as a rule, eat succulent fruits, but Thomson mentions the dispersal of the Sweet-briar (*Rosa rubiginosa*) by horses in New Zealand (*see under* Goats, p. 369), and C. S. Sargent (in " Silva of North America ") states that horses and cattle eat fallen fruits of the *Osage* orange (*Toxylon pomiferum*, *Maclura aurantiaca*) in America. Heinitz gives a list of plants raised from seeds from horse dung in Sweden, showing how large a number of herbaceous plants are disseminated by the horse: *Ranunculus repens*, *R. flammula*, *Myosurus minimus*, *Sagina procumbens*, *Cerastium vulgare*, *Stellaria media*, *Viola* sp., *Medicago falcata*, *M. lupulina*, *Melilotus officinalis*, *M. alba*, and *M. parviflora*, *Trifolium repens*, *T. pratense*, *Lotus corniculatus*, *Gentiana amarella*, *G. campestris*, *Galium verum*, *Achillea millefolium*, *Centaurea Jacea*, *Chrysanthemum Leucanthemum*, *Matricaria discoidea*, *M. inodora*, *Tanacetum vulgare*, *Campanula rotundifolia*, *Euphrasia tenuis*, *Veronica agrestis*, *V. serpyllifolia*, *Primula vulgaris*, *Calluna vulgaris*, *Plantago major*, *P. media*, *Atriplex patula*, *Chenopodium album*, *Rumex acetosella*, *Polygonum persicaria*, *P. aviculare*, *Juncus bufonius*, *Aira coespitosa*, *Alopecurus pratensis*, *Phleum pratense*, *Poa annua*, *P. trivialis*, *P. pratensis*, *Phalaris arundinacea*, *Carex stellulata*, and several other species.

Horses, as well as cattle, constantly swallow spores of fungi on the grass they eat, and pass them in a germinating condition; a large number of the fungi which habitually appear on the dung of these animals are distributed in this way. *Ascobolus* and *Pilobolus* have a mechanism by which they shoot their spores so as to adhere to the herbage (*see* Explosive Fruits, p. 674). Species of *Coprinus*, *Peziza*, *Paneolus*, *Anillaria* and *Galera* are peculiar to the dung of horses and cattle, and the spores dispersed on the grass and herbs these animals eat are passed in the dung, where they develop, having been intimately mixed in the contents of the intestine. E. S. Clayton (*Agric. Gaz., N.S. Wales*, xxxvii, 12, p. 860, 1925) attributed the spread of flag-smut of wheat (*Urocystis tritici*) to feeding horses on chaff made of wheaten hay infected with the disease, as the spores of the fungus pass through the alimentary canal without losing their germinative powers.

Cattle (*Bovidae*. Domestic Cattle, *Bos taurus*).—It was a custom, in the early days of exploring travellers, to carry on board ship cattle, goats, pigs and sheep, and sometimes horses, to remote parts of the world, partly for provision for the voyage, and partly, especially in the case of goats and pigs, to put the animals ashore as future food for later visitors. These animals were provided with hay and other fodder plants taken on board, usually at the

previous port at which the ship stopped. This fodder naturally contained many seeds of grasses and herbaceous plants, and the animals, when brought to land, carried with them in their viscera, or attached to their hair or wool, seeds of various plants in a germinable state, and, again, the manure and waste fodder on the ship was likely to be thrown on shore, or so near it that the seeds could drift on the coast. In these ways many plants have been transported to different parts of the world. Thus I found in 1904, in Christmas Island, after the introduction of a bull and some cows, at least a dozen weeds associated with cattle, which were not found by Andrews in 1897, when the only domestic animal there was a goat.

Strictly speaking, this method of dispersal should be treated as one due to human agency, and further notes on it will be found under that heading (p. 628), but many plants, however they arrived in distant countries originally, are now widely disseminated by cattle more extensively. Some of these weeds are now so extensively distributed, and so much confined to cultivated land, that it is dubious as to what part of the world they originated in.

I deal now with plants disseminated over the land by domestic kine. Heinitz (in the " Food of Animals in Sweden ") gives a very large series of plants disseminated by cattle, the seeds being passed through them in their excreta; all, or nearly all, are herbaceous.

I give a selection from the list:—*Ranunculus repens*, R. *acre*, *Myosurus minimus*, *Thlaspi arvense*, *Malva rotundifolia*, *M. borealis*, *Viola tricolor*, *Cerastium vulgare*, *Stellaria media*, *Sisymbrium Sophia*, *Capsella bursa-pastoris*, *Scleranthus annuus*, *Spergula arvensis*, *Geranium molle*, *G. pusillum*, *Potentilla reptans*, *Alchemilla vulgaris*, *Rosa* sp., *Medicago lupulina*, *Astragalus alpinus*, *Trifolium repens*, *T. pratense*, *T. procumbens*, *Vicia sativa*, *Pisum sativum*, *Ervum tetraspermum*, *Anthyllis vulneraria*, *Daucus carota*, *Pimpinella saxifraga*, *Carum carui*, *Callitriche verna*, *Calluna vulgaris*, *Galium aparine*, *G. boreale*, *G. mollugo*, *G. verum*, *G. palustre*, *Gnaphalium supinum*, *G. uliginosum*, *Anthemis arvensis*, *Matricaria inodora*, *Leontodon autumnalis*, *Artemisia campestris*, *Campanula rotundifolia*, *Plantago lanceolata*, *P. media*, *P. major*, *P. maritima*, *Polemonium coeruleum*, *Gentiana nivalis*, *G. tenella*, *G. amarella*, *G. campestris*, *Euphrasia curta*, *Myosotis arvensis*, *Galeopsis tetrahit*, *Primula vulgaris*, *Veronica arvensis*, *V. Chamaedrys*, *V. hederaefolia* and other species; *Urtica dioica* and *U. urens*, *Atriplex hastata*, *A. patula*, *Chenopodium album*, *Polygonum aviculare*, *P. convolvulus* and *P. persicaria*; *Rumex domesticus*, R. *obtusifolius* and R. *acetosella*; *Sparganium ramosum*, *Juncus bufonius*, and a number of grasses and some sedges, given further on.

If we take this as a typical list of plants eaten and disseminated by an ungulate, we can realise at once how very many small herbaceous plants with small dry fruits and seeds in capsules are so widely spread, and make their appearance so rapidly on bare ground, which otherwise would seem to have no method of dispersal except by a short-distance flight by wind and movement by rainwash. In past time the ungulates were vastly more abundant than at present. Wild cattle occurred, often in great numbers, all over the north temperate regions, and well into the tropics of the Old World. Browsing chiefly on low herbaceous plants, they ate the capsules and dry fruits with them, and passed the seeds uninjured, and are thus responsible largely for the spread of the small *Scrophulariaceae*, *Cruciferae*, *Leguminosae* and *Rubiaceae*. In many parts of the world the wild cattle have been exterminated, and replaced by the domestic cattle, which now play their part as disseminators of herbaceous plants.

Among the soft fruits passed safely and in a germinable state through the cow, as given in this list, we may note, as rather unexpected, *Viola*, and the *Compositae* and *Umbelliferae*, which might not be expected to pass through

the ordeal uninjured. Indeed, in the case of most of these, Heinitz records only a small number of living seed found in the excreta, but the fact that these few survive is enough to account for the spread of the plant.

Among the weedy herbs closely associated with cattle we find that the plants of the genus *Amaranthus* (*Amarantaceae*) are very conspicuous. They are low succulent herbs with numerous small flowers in dense axillary clusters or panicles. The solitary hard, black, smooth seed is enclosed in a small utricle. They are mostly tropical and subtropical, but occasionally appear sporadically in temperate climates, and a number are used as pot-herbs by natives and Europeans. Their home of origin is obscure, but they now occur nearly all over the warmer parts of the globe. They are popular with cattle and horses, and the plants constantly occur in manure heaps or places where cattle are kept.

Amaranthus viridis, now widely spread over the whole world, comes up commonly in cattle and horse dung. I found it in Christmas Island in 1904, near the Settlement and on the paths through the forest where the ponies had been. Andrews did not find it in 1897, when there was only a single goat there, but when, in 1904, a number of ponies, cows, and a bull had been introduced, it appeared. As the cattle did not traverse the steep forest paths, its presence there was undoubtedly due to the ponies, which did. In Fernando de Noronha, where there were no cattle, it occurred by the paths in and round the villages where the horses went, but it was absent from the smaller islands, St. Michael's Mount and Rat Island, where horses had never been. No species of the genus occurred in Krakatau as late as 1919. This species is the only common one in which the utricle does not split and let out the seed. This certainly prevents the seed being accidentally dropped by the browsing animal, and perhaps also protects it from injury when passing through the intestine. It is the most common species of the genus, and the most widely spread. *Amaranthus spinosus*, a species armed with the sharp spines, is more common along the roadsides where the cattle browse in the Malay Peninsula, and Burtt-Davy states (" Alien Flora in the Transvaal ") that it is also common in the Transvaal. It is absent from Christmas Island and Fernando de Noronha. It is probably cattle-dispersed to some extent, but the sharp spines seem to deter them from eating it generally. *A. paniculatus*, according to Burtt-Davy, is the more common species in the Transvaal, and is abundant in cattle kraals and manure heaps. The plant is common in Malaya, but it is a popular vegetable, and forms of it are cultivated as a pot-herb. It only occurred in and round cultivations in Christmas Island and Fernando de Noronha, and mainly in such spots in the Malay Peninsula, but there is no doubt cattle eat it readily. *A. gangeticus* is another weed of cultivation of the same type, but confined to the mainland of Eastern Asia. It is absent from the islands. So far as I have seen, no species is found on any island previous to the introduction of cattle, with the exception of *A. melancholicus* var. *tricolor*, New Hebrides and Tahiti (1768–1780), an ornamental species, also used as spinach, and perhaps *A. paniculata*, carried about as a food plant.

Scoparia dulcis (*Scrophulariaceae*).—Of this now widely-dispersed bushy herb or shrublet, with small white flowers and little capsules full of minute seeds, I have given an account of the dissemination and history in *Annals of Botany*, xxxvii, p. 13. It was first described by Linnaeus from specimens collected in Jamaica and Curacao in 1753, and is undoubtedly of South American and West Indian origin. All the earlier descriptions of the plant are to be found in books dealing with South American plants. However, J. Rotheram, a pupil of Linnaeus, who died in 1804, has written in his copy of Linnaeus' " Species Plantarum," now in my possession, a manuscript note to the effect that the plant was used in Guinea, West Africa, as a drug for venereal disease, showing that it had arrived there before 1804. It was probably carried across

there from South America in ships connected with the slave trade. Chr. Smith records it as found in the Congo, in "Tuckey's Voyage," in 1816; Loureiro met with it in Cochin China in 1773, perhaps brought as a drug by the Jesuit missionaries; Robert Brown found it in Australia in Shoalwater Bay, on the north-east coast, in 1802. It is difficult to see how it got there so early, possibly in cattle fodder, possibly accidentally brought by Malays, or by Cook's expedition. The plant here is a form with very narrow leaves. It first appeared in India in 1843, but seemed to disappear again till in quite recent years it was recovered, and it is still absent from Ceylon. My earliest record for the Malay Peninsula is 1884, but it was probably there much earlier. The Malays call it "Te' Macao" (Macao tea), implying that it came from China. It was collected in Hongkong between 1853 and 1856. It has been used as a drug for phthisis by natives, and has perhaps been carried about by Chinese and others as a medicine. In the Malay Peninsula it is largely disseminated by cattle and buffaloes, which feed on it, and it has travelled farther in Pahang, on the east coast, than any other introduced South American weed, except, perhaps, *Paspalum conjugatum*, a grass widely spread by the attachment of its adhesive glumes to human clothing and the hair of cattle. Wherever buffaloes or cattle went, this plant accompanied them, and was frequently to be seen springing up from their dung. It was noticeably absent from spots where buffaloes had not gone, along the Pahang River. In Africa, too, Mr. Burtt-Davy tells me, it comes up abundantly at the cattle's watering-places. It is probable that it first migrated from the West Indies to Africa in the 18th century, and spread over the country very soon, and was carried from South America to the Philippines by the Jesuits, either accidentally or in cattle fodder, or perhaps as a drug, and thence accompanied the cattle through the Malay Archipelago to the Malay Peninsula and to China. Its absence from Ceylon, and largely from India and from Polynesia, is due to the fact that there was no cattle trade from Africa or the Malay region to these places. It is also absent from Cocos-Keeling and Christmas Islands. As it is obviously still spreading, it will probably reach the countries where it is absent, in a short period of time, in cattle fodder.

Herpestes monniera (*Scrophulariaceae*), a small succulent herb inhabiting wet, swampy and marshy places, edges of pools and rivers in all warm parts of the world, is certainly very widely disseminated by cattle, which browse on the foliage and doubtless swallow and pass the seeds unharmed. It is found in India and Malaya, China, Africa, Cape Verde Isles, Socotra, Arabia, Madagascar, Rodriguez, Diego Garcia, Aldabra, Australia, Moreton Island, all America where not too cold, and Bermuda. It is noticeable that it is largely an island plant, occurring in spots to which cattle are not likely to have carried it, and as it is a marsh plant, we must conclude that, like so many of that class of plant, it is dispersed also by swamp birds.

Wallace (in "Palms of the Amazons") states that cattle eat the pulpy fruits of the Palm *Astrocaryum Muru-muru*, and pass the seeds undigested, so that they are widely scattered over the pastures adjoining the houses, and Standley says that the fruit of *Attalea Cohune* is eaten by cattle in Mexico.

J. M. Cowan (in "Flora of Chankaria, Sundribuns," Rec. Bot. Surv. Ind., xi, 197) says:—"Cattle were frequently driven between the island and main-"land, and *Antidesma Ghaesembilla*, *Ficus altissima*, *Premna bengalensis* and "*Vitex pubescens*, all excellent fodder plants, have either been carried by "cattle or birds." It is quite likely that cattle have played a part in the dissemination of these plants, swallowing the seeds with the foliage, but all, and most especially the *Ficus* and *Vitex*, are largely dispersed by birds.

Euphorbia Drummondii.—This herb in Australia is condemned by some

people as poisonous to stock, but Ewart says it is eaten by cattle, sheep and horses when starved and when travelling, and is thus dispersed.

Cryptostemma calendulacea (*Compositae*), a native of Africa, now introduced into Australia, is troublesome to stock-keepers, according to Maiden, who says the cattle, in feeding, lick up the woolly seeds, which form balls in the stomach.

D. Milne (*Agric. Journ. Ind.*, xi, p. 1), in experimenting on cattle foods, found that seeds of *Asphodelus fistulosus*, *Chenopodium album*, and *Lathyrus aphaca* passed through cattle and successfully germinated, and from 9 to 20 per cent. of wheat-grains passed through, germinated, and produced strong plants. Gram (*Cicer arietinum*), however, failed, practically none growing. The abundance of the *Chenopodium* in farm-yards and cattle-pens in England must be known to everyone.

Anthocephalus cadamba (*Rubiaceae*).—This tree, with its orange-coloured heads of fruits, from 1½ to 2 inches through, is common in India, where its fruits are eaten by bats, and also by man, birds and cattle. Seedlings often come up in considerable numbers in grazed areas or where cattle are herded together.

Gmelina arborea (*Verbenaceae*).—The pulpy yellow drupes, about 1 inch long, of this tree are also eagerly devoured by cattle (Troup).

Strobilanthes (*Acanthaceae*) is a genus of large shrubs abundant in India and Ceylon, growing in the forests in great masses. The cattle eat the plant as fodder, and doubtless swallow the ripe seeds. As the natives say that eating the unripe fruits is injurious to cattle, they will not allow them to feed on the plant till the fruit is ripe. The greater number of the plants of this order disperse their seed by explosion of the capsule, but it is more than probable that the cattle, in eating the plant with its ripe fruit, will swallow the seeds and so disperse them, as is the case of an Acanthaceous plant eaten by the eland, described later (*see* p. 371).

Striga lutea (*Scrophularineae*).—This is a small slender plant from 3 to 6 inches tall, with small tubular flowers, pink, dark red, yellow, or white, which is a root-parasite on grasses. It is common all over the East Indies, usually growing in grass plots or patches of low grass. In Burma it attacked the *Sorghum*, causing much destruction. It also attacked maize, millets, and 13 species of wild grasses. The seeds are very minute, and were found to be disseminated by cattle as well as by water. I have found it growing on grassy spots along roads, through forest where bullock carts had camped, and it was undoubtedly brought by the cattle, which swallowed the seeds while grazing in the plains below (*Dept. Agric.*, *Burma*, *Bull.* 18, 1921).

Juniperus sp.—F. J. Phillips (in " The Dissemination of Junipers by Birds," *Forest Quarterly*, viii) gives a case of a herd of cattle brought from Texas and harboured for a few days in the treeless part of Kansas, giving rise to a small Juniper plantation. Judging by the map, these places must have been about 500 miles apart. It may be doubted whether they carried the seeds internally or whether in mud on their legs.

Among other plants known to be disseminated by cattle feeding on them may be mentioned first *Physalis minima* (*Solanaceae*), a small herb with round berries containing minute seeds, probably originally a native of South America. Mr. Burtt-Davy says that in the Transvaal it is dispersed by cattle, and that seedlings abound in their dung. I found it in Christmas Island after the introduction of horses and cattle in and around the Settlement; and it generally occurs in the Malay Peninsula in cultivated ground where cattle go.

Trifolium repens.—Thomson (in " The Naturalisation of Plants and Animals in New Zealand ") states that white clover seed passes undigested through the stomachs of cattle, for it is common to find it germinating in their dung. It has also been known to be similarly dispersed by Yaks in Thibet.

Opuntias.—W. B. Alexander (in " Prickly Pears Naturalised in Australia ") says that the animals and birds which distribute the Cacti are cattle, pigs, wallabies, emus, crows and bell-magpies, and records that of one species of *Opuntia* introduced by Mr. Birkbeck in 1857, his son fed the fruits to pigs, which carried the seed all over the estate, and apparently much farther. Cattle also aided the dissemination of this plant. The species introduced, which have run wild in Australia, were 17 species of *Opuntia*, two species of *Nopalea*, and one species of *Anthocereus*. Johnson also includes cattle as dispersers of *Opuntia decumana* in South Africa.

Berberis vulgaris (Barberry).—The well-known barberry is a bush with small brilliant red berries which are acid, and, apparently for this reason, are not popular with birds. It appears, however, not to be correct to say, as is sometimes said (e.g., Sowerby's " English Botany ") that birds will not eat them, as blackbirds occasionally do. The plant was introduced into America from Europe early, by settlers, for its fruit to make jelly, and F. D. Kern (in " Observations on the Dissemination of the Barberry," *Ecology*, ii, p. 211) describes its spread in America by cattle. He points out that Rhind in 1857 (" History of the Vegetable Kingdom ") states that cattle, sheep and goats browse on this shrub, and says that in several places where old persons could recall the time when a barberry bush at a door-yard was a novelty, barberries are now too numerous to estimate. He found numerous seedlings growing from cow dung; as many as 45 were found in a single dropping. The cattle browsed the foliage and ate the berries as well. Shady places, evidently stamping grounds for cattle, were covered with young bushes. In one corner of a pasture under a large tree, which was a congregating spot, 145 bushes of various sizes were noted. An article (in the Cereal Courier, U.S.A., vol. ii, p. 327) also describes the dispersal of this plant by cattle in Wisconsin.

Philippi (in Peterman's Mittheil, 1886, x, i, 298) says that the apple is spreading in millions in Chile, the seeds passing through the dung of cattle. Of this, J. Ball writes (*Journ. Linn. Soc.*, xxi, 217) :—" The apple is said to have " been introduced into this region (North Patagonia) by the Spanish " missionaries. It has thriven wonderfully, and in the interior, between " 40° S. and 40·30, it forms extensive groves and even small forests. It has " developed two varieties, one sweet and the other somewhat tart, but not " uneatable." It is rather remarkable that the apple has not run wild elsewhere, being so constantly cultivated and the seeds often thrown about. I have no other records than the above of a wild form appearing anywhere, and the only escaped one that I remember to have seen was one on the Thames river bank at Kew Bridge.

Cucumis melo var. *agrestis*.—This wild African melon is eaten by domestic cattle in the Kalahari desert, South Africa, as are also the small wild forms of the Water-melon (*Citrullus vulgaris*), I am informed by Mr. Burtt-Davy. They probably eat these for the sake of the water contained in the fruit. The hard seeds are no doubt passed unharmed.

Acacia.—The pods of these trees are always popular with cattle, as well as with goats and sheep. Mr. Burtt wrote me that in the Tanganyika district of Africa his cattle would stop under trees of *Acacia spirocarpa* and browse the fallen pods which lie on the burnt grass beneath the trees. He has also found the seeds passed out in their dung, and noted that wherever cattle, that have grazed in woods of the *Acacia*, are stabled on land of another type of bush, thickets, etc., it is noticeable that young trees of *A. spirocarpa* spring up near by. The pods of this species are about 2 or 3 inches long, flattened and coiled in a spiral, somewhat thick. He noted that his cattle ate the fruits of other species of *Acacia* as well, and also found seeds of *Albizzia hypoleuca* in the

excreta. Marloth says that in South Africa the pods of *Acacia giraffae*, *A. Karroo*, and *A. detinens* are all eaten by cattle. Troup states that in India the pods of *Acacia arabica* are readily eaten by sheep, goats and cattle, but only the latter animals pass the seed safely through the intestine. Of *Acacia Farnesiana* Guppy says that in Hawaii :—" Regarded by Hillebrand as of early intro- " duction, it has spread all over the islands, and in places forms extensive " coastal thickets. Cattle spread the seeds over an island, where they may be " seen germinating in the dung."

This has a very thick fleshy pod compared with the other species, and appears to be first introduced to an island by sea-transport and then disseminated by cattle.

Leucaena glauca, a widely-distributed shrub or small tree, probably originally a native of South America, was introduced into Rodriguez about 1849, according to I. Bayley Balfour (Phil. Trans. Roy. Soc. Lond., 1879, p. 303). It now covers the ground for many acres, owing its spreading in a great measure to the cattle and goats, which are exceedingly fond of its leaves and pods, and thus carry the seeds about. *Lespedeza striata* is another Leguminous shrub disseminated by cattle. It was introduced into North America from China as a fodder plant, and is largely dispersed by cattle in the Gulf States, according to C. Mohr (*Bot. Gaz.*, iii, 43). He says that one of the principal causes by which the rapid spread of this plant has been effected was the transfer of beef-cattle following through the South the movements of the armies (this was in the American Civil Wars of 1860). He writes :—" I found almost invariably " the plant springing up from the decayed droppings of cattle."

Phaseolus sp.—Sir David Prain found seedlings of a species of vetch of this genus appearing in the droppings of half-wild cattle in Little Coco (Andamans). He was unable to procure fully developed plants, and no species of the genus is recorded from the island. No doubt the cattle ate the whole plant, pods and all, and passed the seeds.

Inga Saman.—This tree, now widely scattered over the tropics as a roadside or ornamental tree, is a native of South America, and is popularly known as the Rain Tree. The pods, which are 6 inches long and 1 inch wide, and flattened, contain a number of flat seeds enclosed in a sweet treacly substance which is much liked by cattle, and, indeed, forms a valuable food for them. As the tree is a tall one, they eat the fallen pods lying on the ground. According to Grisebach (" Flora of the West Indian Islands," p. 225), the seeds were brought over from Jamaica from the mainland by cattle, and naturalised there. Formerly, says Morris (*Nature*, xxxvii, 466), Jamaica and Trinidad depended for their cattle on Venezuela. These cattle were fed on the pods of the Rain Tree with other food, and on their arrival the seeds were passed in the pastures, germinated, and grew into trees. In this instance the seeds were transported across the sea for a thousand miles—a very good example of the migration of a plant due to cattle. Spruce, in a note on a specimen in the Kew Herbarium, says that in South America cattle and deer eat the pods as soon as they fall, and the plant is locally called " Deer's vanilla," no doubt an allusion to the form of the fruit.

Prosopis juliflora, the Mesquit Bean of South America, has pods of a sweet succulent nature, eagerly sought by cattle. Indeed, in some parts of Jamaica they subsist largely on it in droughts (Troup). W. L. Hall (in " Forests of the Hawaiian Islands ") writes that the pods fall to the ground and are eaten by cattle, horses, and pigs. The stock do not crush the small horny seeds, which pass through the alimentary canal and are prepared for quick germination by the action of the digestive fluids. Stock are therefore solely responsible for the rapid and wide spread of this tree. Alexander Prior says (in Herb. Kew) that the seeds in Jamaica are fatal to horses, as they germinate very

rapidly in their stomachs, but in Pretoria the pods are said to be a favourite food of children, goats and cattle (W. Cillier, in Herb. Kew). This species occurs in the Galapagos, where Darwin found it in 1835. There were settlers on the islands then, but he only records wild pigs and goats as domestic animals there (in the " Voyage of the Beagle ").

There are a number of species of *Prosopis* very widely spread over the warm dry regions of the world, but they seem to be most abundant in South America. One species, *P. Stephaniana*, is found over Persia and North India, and there are several others in Africa, and one in the Cape Verde Islands, *P. chrysocarpa*. *P. dulcis*, the Algaroba of South America, *P. glandulosa*, Mesquit of Texas, and *P. pubescens*, the screw Mesquit of Texas and New Mexico, and *P. spicigera*, of India, are all used as cattle food. There can be little doubt that it is due to the sweet pulp of the pods of *Prosopis* that the genus is so widely spread and abundant in suitable areas.

Sedges (*Cyperaceae*) are probably dispersed by cattle, at least to some extent, but as their foliage is rather harsh and stiff, they do not seem so popular. Of the 3 sedges found in Christmas Island by me after cattle had been introduced, 2 are sea-dispersed, and *Cyperus Iria*, which was possibly introduced in rice, was the only other. *Fimbristylis miliacea* and *F. globulosa* are said by the Malays to be distributed by cattle and buffalos, and Maiden notes that the seeds of *Cyperus rotundus* have a hard coat, and do not yield to digestion in the case of ordinary farm animals, except sheep, which I understand destroy them. Heinitz, in his account of plants disseminated by cattle in Sweden, gives *Carex flava*, *C. panicea*, *C. canescens*, and *Scirpus lacustris* as found in the excreta.

Grasses.—Many grasses are distributed by cattle eating the panicle with the foliage and passing the grains uninjured, but probably more are so passed by horses, deer, and antelopes.

Among those that are commonly disseminated by cattle is *Echinochloa colona* (*Panicum colonum*), which often springs up from the dung of cattle. It is widely spread all over the tropics and subtropics, and occurred near the Settlement in Christmas Island in 1904, after the introduction of cattle. *Imperata cylindrica*, the Lalang, is another grass disseminated by cattle, though it is more commonly spread by its plumed fruits. Still, I have seen it coming up from seed in cattle manure, in Singapore. *Bromus sterilis* is also spread in the same way, both by cattle and horses, in England. *Eleusine indica.*—Prain records finding in Coco Island (Andamans) a few tufts of this very common grass among the droppings of cattle, and I have little doubt that it owes much of its wide distribution to this source; but that it has other methods of dispersal is shown by its appearance in Christmas Island, where I found it in 1890, before cattle or horses came, and it had reached Krakatau by 1919, where there were no cattle or horses.

Melocanna bambusoides.—This large-fruited Bamboo is said by Troup to be dispersed by cattle in India.

Panicum barbinode (*P. muticum*), the Para Grass, or Water Grass, is a world-wide species of which it has been shown that, wherever cattle are fed on it, the joints of the stems even after passing through the animals, continued to grow, so that it proved a nuisance and very troublesome in sugar estates.

Pennisetum clandestinum, the Kikuyu Grass, of Mount Kenya, East Africa.—This is a low-creeping and branching grass, which bears its fruits low down, almost on the ground, the spikelets being produced in short leaf-tufts. When the seed is procured by simply beating the dry grass, it is extremely difficult to separate the grain from the glumes. (This suggests that originally this grass was dispersed by wind blowing along the ground, as is usually the case when the glumes are firmly attached to the grain, and act as wings.) Mr. Lyne

Watt (*Kew Bulletin*, 1925, p. 403) from whose account of this grass I take these notes, continues :—

" In Kenya it is a common sight to see seedlings in fresh cultivated ground " where cattle, after grazing over Kikuyu Grass, have passed and dropped " their dung. This is a great nuisance in young forest plantations, where " the native herds often stray from their pasture."

Heinitz gives the following grasses as coming up from cattle manure in Sweden :—*Alopecurus fulvus* and *A. geniculatus*, *Festuca rubra*, *Phleum pratense*, *Poa annua*, *P. trivialis*, *P. pratensis*, *Agrostis vulgaris*, *Avena sativa*, *Hordeum vulgare*, *Bromus secalinus*.

Fungi.—The spores of many fungi are swallowed by cattle in grass-eating and dispersed in the dung, as is described under the account of Horses (*see* p. 306).

Yak (*Bos* (*Poephagus*) *grunniens*).—Hooker (in the *Himalayan Journ.*, chap. xxii) writes of the Donkia Pass in Thibet :—" White clover, Shepherd's Purse, dock, " plantain and chickweed are imported here by Yaks."

Bos Gaurus, the Indian Bison, Gaur, or Seladang of the Malays, wanders over the wooded districts of Assam, Burma, Indo-China and the Malay Peninsula. This large ox lives chiefly in dense forest of the lowlands, and is reported to feed largely on fallen fruit in the Malay Peninsula. A captive one in Singapore ate bananas and other fruit readily. Troup says it eats the fruit of *Melocanna bambusoides*, but the natural history of this animal appears to be little known.

Bubalus Arnee, the Water-Buffalo of Malaya, is certainly responsible for the dispersal of many seeds of herbaceous plants. Along the Pahang River I found *Cleome viscosa* and *Scoparia dulcis* occurring on all the sand-banks and other spots where the water-buffalos go, and the latter plant I found growing from the dung. *Herpestes monniera* is also almost certainly disseminated by them, and probably most of the herbaceous plants on these sandy plains are dispersed by them, as cattle are absent from these places.

Bubalus caffer, the Cape Buffalo, seems to feed chiefly on grass, and I have no record of any plants being seen springing up from the dung. D. D. Garnett (in *Country Life*, October 1st, 1927) writes of the Semliki Plains in Uganda :— " Early in the afternoon the buffalo would cross the streams and move across, " to disappear among the Palms (*Borassus aethiopum*), whose juicy yellow " fruits seem to attract them." The seeds are too big for these animals to swallow, so they are hardly likely to disseminate the Palm as the elephant does, but the observation suggests that they also eat juicy fruits as well as grass.

Bison americanus, the American Bison (often called the buffalo in America), before it was nearly exterminated, was probably one of the most important seed-dispersers of the herbaceous plants, by swallowing the seeds in feeding and passing them unharmed, as do other cattle, but I have found little information about this. R. Miller Christy (in his notes on the " Flora of Manitoba," *Journ. Bot.*, 1887, p. 290) gives an account of seeds dispersed by adhesion to the long hair of this animal (dealt with under Fruit and Seed Adhesion to Animals, p. 532), and mentions one Leguminous plantal most certainly dispersed by bison eating the pods, *Astragalus corynocarpus*, the Buffalo-Bean. The pods, which remain green and succulent when the seeds are ripe enough to rattle, are very popular with cattle, and as the range of the plant agrees fairly well with the former range of the bison, it would appear probable that the plant was eaten and the seed dispersed by them.

M. Hornaday (in Bull. Soc. d'Acclimatation, 1894, p. 357) gives an account of the food of the bison, which he says eats many grasses and *Atriplex canescens*, of which it may pass the seeds. The grasses it is particularly fond of are *Bouteloua oligostachya*, *Buchloe dactyloides*, *Stipa sparta* and *S. comata*, *Aristida*

purpurea, *Koeleria cristata*, *Poa tenuifolia*, *Festuca scabrella*, *Andropogon provincialis* and *A. scoparius*, *Agropyrum divergens* and *A. caninum*. It may pass the grains of some of these unharmed, and in some of them the fruits would adhere to its hair and so be carried about.

Goats (*Capra hircus*).—Mr. Burtt-Davy tells me that in South Africa *Datura stramonium* is dispersed by goats, which eat it. This plant is poisonous to most animals. It is a native of South America, now spread over the world as a weed, though absent from tropical regions. It frequently appears sporadically in England, on rubbish heaps and waste ground. The fruit is a spiny capsule, which dehisces and lets out a number of flat, dry, poisonous seeds.

Heinitz has found in Sweden the following plants eaten and their seeds distributed by goats—*Capsella Bursa-pastoris*, *Plantago major*, *Rumex acetosella* and *Veronica serpyllifolia*.

E. A. Weston (in the *Agric. Gaz.*, *New South Wales*, xiii, 1902, p. 213) states that the fruits of the Sweet-briar (*Rosa rubiginosa*) caused the death of a number of goats in Tasmania. They ate the fruits, and the hairy coat of the seeds caused their death by forming hairy calculi which occluded the lumen of the intestine. The goats had been introduced into the region to exterminate this plant, but, though they effected this, the plant also exterminated them. Cattle, he states, are also very fond of the briar berries, and from time to time one will die, but the hairy calculi do not form in the stomach, though their various stomachs are one mass of the briar seeds. Thomson (" Naturalisation of Animals and Plants in New Zealand ") says that the sweet-briar is largely spread by horses, which eat the hips, but do not digest the achenes. I have no record of any of these animals eating the fruits of any of the roses in England, though birds eat them, but probably do not swallow the seeds. It is remarkable that they should be so fatal to goats, and not to cattle or horses. The hairs on the seeds are very irritating, and when, as children, we used to eat the fruit, we squeezed the sweet juice into our mouths from the base of the fruits, taking care not to get the irritating seeds into our mouths.

The dispersal of seed of *Acacia arabica* in India by goats eating the pods, and the custom of feeding goats on them in order to hasten germination, has already been stated under the heading of the Germination of Seeds hastened by passing through an animal (*see* p. 338).

Troup, however, states that the sheep and goats do not swallow the seeds of *Acacia arabica*, but eject them after rumination. He says that, where possible, seeds should be collected from sheep and goat pens, as these seeds germinate more readily and with a higher percentage of success. He says also that goats eat the fruit of *Terminalia belerica*, and so disseminate the seeds. *Leucaena glauca* is also said to be disseminated by goats, as has been mentioned.

Hippomane mancinella (*Euphorbiaceae*), the Manchineel, occurs on the sea-coasts of the New World in the West Indies, and on the Atlantic coasts from Mexico to Venezuela, and on the Pacific coasts. It is usually found, according to Guppy, on the sandy soil bordering the beach. Millspaugh says it grows in coppices and on scrubland in the Bahamas, and Harshberger says it grows inland in Florida. It is undoubtedly a drift fruit, as Guppy shows, but he has seen no germinating fruit on the beach-drift. He suggests that the intervention of land-crabs may be necessary, and that germination only occurs after the fruit has been stored in their burrows. Sloane (" Voyage to Jamaica," ii, 4, 7) says that goats feed on the fruits readily, and he was shown trees that had grown from seeds contained in their dung.

Lewis, in Ceylon, states that *Commelina zeylanica* grows frequently by detached bits, and is probably spread by goats, as they have also spread *Mimosa pudica*. I have never seen any animals eating the latter plant; cattle and horses

avoid it. *Commelina nudiflora* is certainly a popular fodder with all animals, and is common on manure heaps. In all probability it is eaten and the seeds passed by cattle of all kinds.

Guppy says: "The agency of the wild goat explains the dispersal of "*Myoporum sandwicense*, *Morinda citrifolia*, *Tephrosia piscatoria*, *Waltheria americana*, "etc., over the almost bare lava flows of the Puna Coast (Hawaii). Goat "droppings were frequent under the patches of *Myoporum* and *Waltheria*. "In some of them I found the entire seeds of *Portulaca oleracea* and the small "cocci of *Euphorbia pilulifera* (*E. hirta*), weeds common in the district." He also records the droppings as common in the beach-drift, and says they can float for some weeks before breaking down.

The seeds of the Cactus *Opuntia decumana* are swallowed with the fruit, and dispersed by goats and other domestic animals in South Africa (Johnston). Indeed, most of the plants eaten by cattle, and especially the herbaceous and shrubby ones, are eaten by goats.

Sheep (*Ovis Aries*).—Guppy records the dispersal of seeds of *Morinda citrifolia* in Cocos Island by sheep as well as by deer and fowls, etc.

In Africa the sheep, like goats and cattle, appear to eat the pods of *Acacias*, and Marloth mentions their feeding on those of *Acacia Karroo* and *A. detinens* and *A. giraffae* in South Africa.

Livingstone (in his "Missionary Travels," 1857, chap. v.) writes:—"In the Kalahari desert the ground was said to be covered with a coating of "grass, which disappeared with the antelopes that fed upon it, and *Mesembry-* "*anthemums* and *Crassulas* replace it. As this vegetation is better adapted for "sheep and goats in a very dry country than grass, the Boers bring a few "waggon-loads of *Mesembryanthemums* in seed and place them where the sheep "have access in the evening. As they eat a little every night, the seeds are "dropped over the grazing ground, and the place becomes a sheep farm, as "the animals thrive on such herbage." It is, indeed, most probable that these succulent herbs are conveyed and spread about the whole dry region of Africa by the herbivorous Mammals.

H. C. Long (in "Weeds in Arable Land") associates *Polygonum aviculare* with sheep, stating that it occurs on soils heavily manured by them. Sheep undoubtedly, moved about in flocks, have played an important part in transporting seeds internally, as cattle, horses, and goats have done, but their most important dissemination has been due to their carrying seeds and fruits in their fleeces.

Giraffe (*Giraffa camelopardalis*).—"Giraffes show great liking for the fruit "of *Acacia spirocarpa*, as seeds of this species were usually present in the "faecal pellets. Individual pellets contained from 1 to 4 seeds, while the seed "of *Randia nilotica* was commonly found in them" (Burtt). They are also recorded by other writers as eating the pods of *Acacia giraffae* and *A. Durazzi*.

Antelopes.—It is probable that the vast herds of antelopes in Africa play a considerable part in seed-distribution, but I have comparatively little information on the subject. Mr. Burtt-Davy tells me that the antelopes of the Kalahari desert eat the wild African Melon (*Cucumis melo* var. *agrestis*), and doubtless disperse the seeds. *Hippotragus niger*, the great Sable Antelope.—Mr. Johnston (in Contrib. Asa Gray Herb. 3, lxxiii, 33, 1924) describes a dwarf leguminous shrub from 6 to 12 inches tall, *Cryptosepalum Curtisiorum*, which he says forms the food of this animal.

The Eland (*Taurotragus oryx*).—Mr. Burtt in his report says: "The "stomach contents of several eland were examined, usually revealing many "seeds of various species of *Acacia*," of which he mentions *A. spirocarpa*, *A. pallens*, *A. verugera* and *Dichrostachys glomerata* (*Leguminosae*) as found in the stomach and dung. On one occasion the seeds of *Adansonia digitata*, and on

another those of *Strychnos pungens* were found. In the latter case the seeds had been, in some instances, crushed and injured, so that the value of the eland as a dispersal agent of this species is doubtful. In another case the fruits of a small spiny *Acanthaceous* plant, *Blepharis Buchneri*, were found in great numbers; when dried out, the fruits exploded in the normal manner of the order. It seems evident that the eland accidentally eats the fruits of this plant when browsing upon the dry heads of the plants. The capsules were found undigested in the large intestine of the animal, though the prickly bracts were quite digested and gone.

The Impalla Buck (*Oepyceros Melampus*).—Mr. Burtt records finding grass seeds in the stomach of this antelope, as also seeds of *Acacia spirocarpa*, *Randia nilotica* (*Rubiaceae*), a shrub, and *Solanum xanthocarpum*. The seeds of the *Acacia* and the *Solanum* were specially abundant in their stomachs.

Saiga Antelope (*Saiga tatarica*).—In the steppes of Siberia this antelope feeds on bushes of *Artemisia*, *Atriplex*, *Glycirrhiza* and *Inula dysenterica*, and no doubt swallows and disperses the seeds of some or all of these plants.

Gazelles, Isabelline Gazelle (*Gazella isabella*).—Chapman (in "Savage Sudan," p. 372) writes :—"The isabelline gazelle had been feeding on the "small red berries of a kind of Berberis" in the Red Sea hills. This was probably *Berberis Forskalii*, the only species recorded from that area.

Loder's Gazelle (*Gazella leptoceros*) is said to feed on the leaves and berries of the few desert plants in Arabia and Egypt.

Thompson's Gazelle (*Gazella Thompsoni*).—Burtt writes :—"On the 'examination of the stomach contents of one Thompson's gazelle, shot near 'Twumbu, 5 seeds of *Balanites* were found in the large stomach. The problem 'as to how the seeds were expelled was the cause of much debate, as the 'individual seeds are large, measuring from 1 to 2·7 inches long. At Magun, 'where the antelopes abound, many faecatoria were examined, but no instances 'of the seeds actually occurring in the form of faecal pellets were observed. 'Numerous instances of clean dry seeds were seen, the seeds occurring in 'heaps of from 50 to 100 or so. A reasonable theory would be that the gazelle 'has a liking for the fruity middle coating of the seed, and swallows the whole 'fruit. The fruity layer is then removed in the process of digestion, and 'the cleaned seed regurgitated on to the deposits or in separate heaps." Even in such case as regurgitation of the seeds, the animals might carry them for some distance before doing so.

Seeds of *Acacia verugera* and *A. pallens* and of *Solanum xanthocarpum* were also found in their stomachs.

Deer (*Cervidae*).—The Red Deer (*Cervus elaphus*) and Fallow Deer (*Cervus dama*) eat a quantity of acorns, and in so doing destroy a large amount, but in moving about they tread some into the ground, where they germinate. Pigs are said to do the same, and it is said that the scanty supply of Oak seedlings in forests nowadays is due to the absence of the herds of pigs, and probably to the deer, which formerly fed in the forests (*See also* p. 359.) I have seen fallow deer in Cobham Park, Kent, standing on their hind legs and shaking the branches of hawthorn trees with their antlers to get the fruit.

Spittal ("Wild Life in Ceylon") says that Deer (Sambur), *Cervus aristotelis*, are fed on the fruits of *Mimusops hexandra*.

Troup states that the fruits of *Terminalia belerica* and *Gmelina arborea* are eagerly devoured by deer in India. Of *Aegle marmelos* (*Rutaceae*) he says that the fruits are globose, and green to yellow when ripe, from 2 to 4 inches through, with a hard woody rind and numerous seeds in a mucilaginous pulp. The fruit has a great reputation as a dysentery medicine, and is known as the "Bael Fruit," and is often planted for this purpose, and at one time trees were planted in all the police station grounds in Malacca, by the Government, for the use

of the villages. It is certainly a native of India, and possibly of Siam, but where else it occurs it has been planted by man. Troup says the fruits are often broken open by deer with their hoofs, and that pigs, monkeys, and perhaps bears and jackals, eat the pulp. Seedlings are also found in the forks of trees, showing that birds eat the pulp as well. If the fruit is not broken, the seed perishes, and the plant cannot be reproduced. As the woody rind is very hard, it is impossible for the birds to obtain the pulp unless the fruit is broken up by some powerful mammal. *Spondias mangifera* (*Anacardiaceae*).—This fruit is greedily eaten by deer, pigs, squirrels, and monkeys, and the large bare stones, with the flesh removed, may be found scattered about the forest, from the time the fruit ripens, onward. Small heaps of these stones are continually met with where deer have lain ruminating and bringing them up. The seeds of stones collected from these heaps have been found to germinate well (Troup). This is one of the trees known as the "Hog Plum." The drupe is 2 inches long, yellow, and 1-seeded. The tree is often planted in the East.

Morinda citrifolia.—Guppy records the dispersal of seeds of this plant by deer in Cocos-Keeling Island. *Inga Saman*.—According to Spruce, in a note in Kew Herbarium, the pods of this tree are eaten by deer as well as cattle, in South America, and it is known as Deer's Vanilla. (*See* p. 366.) *Putranjiva Roxburghii* (*Euphorbiaceae*).—A tree with light grey, normally 1-seeded, occasionally 2-seeded, drupes ½ inch long, which are eaten by deer. The hard stones are disgorged by them during rumination. A native of India and Ceylon. *Phyllanthus emblica* (*Euphorbiaceae*) has a globose acid fruit, with from 4 to 6 hard cocci, each containing 1 seed. These are eaten by deer, and, like the last, the seeds are disgorged during rumination, after which the cocci dehisce (Troup). This is a native of India and Ceylon, and a very closely allied species occurs in the Malay forests, where I have seen abundance of fruit lying at the foot of the trees untouched by any animal, but deer were not common there. *Ficus glomerata*.—The figs, when fallen, are a favourite fruit with deer (Troup). *Melocanna bambusoides* (*Gramineae*).—This bamboo has the grain included in a pericarp from 3 to 5 inches long and from 2 to 3 inches wide, filled with starch. It is pear-shaped, and is readily devoured by several animals, including deer, according to Troup. All these, being borne on lofty trees or tall bamboos, can only be picked up from the ground by the animals when fallen.

A. S. Sampson ("Native American Forage Plants," 1928) says that in Western America deer, elks, and other game are fond of the leafage and fruit of *Rosa Fendleri*. Heinitz gives an account of the plants eaten by the red deer, fallow deer, roe deer, and elk in Sweden, of which plants seeds have been found in, and often raised from, the excreta.

Red Deer (*Cervus elaphus*).—*Chenopodium album*, *Galium aparine*, *G. mollugo*, *G. uliginosum*, *Polygonum aviculare*, *Scleranthus annuus*, *Spergula arvensis*, *Trientalis europea*, *Phleum pratense*.

Fallow Deer (*Cervus dama*).—*Carex* sp., *Chenopodium album*, *Galium mollugo*, *G. aparine* and *G. uliginosa*, *Polygonum aviculare* and *P. persicaria*, *Rumex crispus*, *Stellaria media*, *Trifolium repens*, *Viola tricolor*, *Spergula arvensis*, *Plantago major* and *P. media*, *Urtica dioica*, *Poa annua*.

Roe Deer (*Cervus capreolus*).—*Daucus carota*, *Fagopyrum esculentum*, *Chenopodium album*, *Medicago lupulina*, *Plantago major*, *Polygonum aviculare*, *P. persicaria*, *Myosotis arvensis*, *Stellaria media*, *Juncus bufonius*, *Poa annua*, *Agrostis* sp.

Elk (*Alces machlis*).—Heinitz has found in the excreta seeds of *Betula verrucosa*, *Rhamnus frangula*, *Rubus idaeus*, *Comarum palustre*, *Trifolium pratense*, *Andromeda polifolia*, *Calluna vulgaris*.

Reindeer (*Rangifer tarandus*).—This animal, in feeding on the low vegetation of the Arctic region, must swallow and pass in its excreta many of the seeds, which are thus disseminated by it. It is said by Ekstam and Hart to be very partial to *Stellaria longifolia*, of which it certainly disseminates the seeds, and Ekstam, in Spitzbergen, found it dispersing the seeds of *Polemonium pulchellum*. Heinitz gives a long list of the plants it eats and of which the seeds have been found in its excreta. They are as follows :—*Ranunculus acris*, *R. repens*, *R. auricomus*, *R. flammula* var. *reptans*, *R. hyperboreus*, *R. glacialis*, *R. lapponum*, *R. platanifolius*, *R. pygmaeus*, *R. sulfureus*, *Thalictrum alpinum*, *Trollius europaeus*, *Sagina Linnaei*, *Cerastium alpinum*, *C. vulgare* var. *alpestre*, *Stellaria alpestris*, *S. longipes*, *Draba hirta*, *Viola biflora*, *Sibbaldia procumbens*, *Rubus chamaemorus* and *R. arcticus*, *Potentilla verna*, *Montia fontana*, *Chrysosplenium alternifolium*, *Vaccinium* sp., *Astragalus alpinus* and *A. oroboides*, *Rumex acetosa*, *Empetrum nigrum*, *Menyanthes trifoliata*, *Juncus biglumis*, *J. filiformis*, *Luzula multiflora*, *L. parviflora*, *Carex alpina*, *C. atrata*, *C. festiva*, *C. rigida*, *C. persooni*, *C. irrigua* and *C. lagopina*, *Agrostis borealis*, *Festuca ovina*, *F. rubra*, *Catabrosa algida*, *Milium effusum*, *Nardus stricta*, *Vahlodea purpurea*, *Phleum alpinum*, *Poa alpina*, *P. pratensis*, *Polytrichum commune*, *Veronica longifolia*, *V. scutellata*, *V. borealis*, *Euphrasia latifolia*, *Myosotis sylvatica*, *Oxytropis lapponica*, *Phaca frigida*, *Polemonium campanulatum*.

L. J. Palmer (in the "Progress of Reindeer Grazing in Alaska") gives a long list of the plants on which the reindeer feeds, of which the following may very well be disseminated in its excreta :—*Ledum decumbens* and *L. groenlandicum*, *Vaccinium Vitis-idaea* and *V. uliginosum*, *Empetrum nigrum*, *Ranunculus Pallasii*, *Lupinus arcticus*, *Astragalus alpinus* and *A. littoralis*, *Polygonum alaskanum*, *Rumex occidentalis*, *Rubus arcticus*, *R. chamaemorus*, *Ribes triste*, *Viburnum pauciflorum*, *Arctostaphylos alpinus*, *Lathyrus maritimus*, *Coelopleurum Griffithii* (*Archangelica*).

Hyrax (*Hyracoidea*) (*Procavia capensis*).—Marloth (in the "Flora of South Africa," vol. ii) says of *Weissia argentea* (*Anacardiaceae*), the tough and leathery pericarp of the fruit is eaten by the Rock-rabbits (*Hyrax capensis*), which, in doing so, carry the seeds about and distribute them. The seeds themselves, which are bitter, are only eaten by them in times of scarcity.

Rats (*Rodentia*).—These animals usually destroy seeds by gnawing them to pieces, but in some cases do good work in disseminating them by merely carrying them to some distance from the tree and accidentally dropping them. They also eat juicy fruits and scatter the seeds about. In the Malay Peninsula I have seen a number of specimens of an orange-coloured rat, *Mus surifer*, eating jungle mangos which had fallen from a tree. They probably carried the fruits to some distance before eating the pulp. The small yellow or green berries of the various species of *Melothria* and *Mukia*, low-creeping *Cucurbitaceae* in the Malay Peninsula, are carried off and eaten by these animals. *Curculigo* (*Hypoxidaceae*), a large-leaved herb, with soft green sweet fruits hidden away among the leaf-stalks, are taken away by rats. The seeds are small and probably not injured by them, and the fruits of many of the *Zingiberaceae*, *Amomum*, *Zingiber*, etc., are dull-coloured and inconspicuous, and some of them possess small sweet arils on the seed, which are attractive to them. In *Nicolaia* the showy head of flowers is borne on a stalk from 2 to 3 feet tall. The fruits, about 1 inch long, are green and rather hard, and contain a quantity of small stony black seeds. The fruit is always gnawed into, and the seeds scattered about, but whether by rats or squirrels I have been unable to determine. *Scirpodendron costatum* is a Cyperaceous plant forming a thick clump of narrow stiff leaves like those of a Pandanus. It grows in very wet spots, usually in water near the sea or a tidal swamp, in the Malay region and Ceylon. The fruit is an oblong corky brown nut about ½ inch long, of which several are

borne on an erect spike shorter than the leaves. I have constantly found these fruits on the spike gnawed by some rodent, probably a rat, as the habitats are too wet for squirrels, and very frequently all the fruit is carried off. The fruit is really adapted for sea-dispersal, but the plant, so far as I have seen, grows in the thickets in brackish pools or swamps, not distinctly connected with them. I have failed to find any fragments of the vanished fruits near the plant, so that the rodent must carry them clean away.

In Christmas Island, when discovered, there were two species of endemic rats, *M. nativitatis* and *M. maclearii*, and these were in enormous abundance. They only left their holes at night in search of food. Andrews stated that *M. maclearii* could climb trees quite well, and used to come into collision, on the *Papaya* trees, with the local fruit-bats, both feeding on the fruit, and doubtless disseminating it. At the time of my second visit, 1904, the common European rat had been introduced, and though it had not extended its range very far from the Settlement, nor was very abundant there, it had completely exterminated the other two species apparently over the whole island, probably by the accidental introduction of some bacterial disease. Abundance of rat food, consisting of fruits of *Inocarpus edulis* (*Leguminosae*), the Otaheite Chestnut, *Terminalia catappa* (*Combretaceae*), *Ochrocarpus ovalifolius* (*Guttiferae*), were lying about untouched, though I did see under a rock a quantity of fruits of the latter tree, which had been gnawed by rats. These fruits are all sea-dispersed, but on reaching the island they formed food for the rats, who transported them from place to place. This work was carried on by the land-crabs after the disappearance of the endemic rats.

Rats often, like squirrels, only partially eat acorns and other seeds with large cotyledons, and do not injure the seed sufficiently to prevent its germinating. I have seen the acorns of the Turkey Oak (*Quercus cerris*) and the seed of *Aesculus californica* and *A. hippocastanum* nibbled, apparently by rats, and abandoned. In the case of the *Aesculus*, the seed was carried to some distance from the tree. In most cases, perhaps, the seed is too much injured to develop, but in many, though nibbled even till one cotyledon was destroyed, the radicle was still pushing down into the soil. That such seeds are not always destroyed by the rodent I can show in the case of a squirrel, *Nanosciurus exilis*, which I saw on one occasion running across the grass plots in the Singapore Botanic Gardens with something white in its mouth. I pursued it, and it dropped a seed of *Pithecolobium lobatum* (*Leguminosae*), which it had carried off from a tree about 100 yards away. This is a large, round, flat, dark brown seed measuring about 2 inches across. The squirrel had nibbled off all the brown testa, and the large cotyledons were gnawed all over, yet the seed was so slightly injured that, on being planted, it readily germinated and grew. Thus the large fleshy cotyledons of a fruit may, in spite of the rodents, actually aid in the dispersal of the species.

In describing the forms of seed arils I have given some account of the waxy arils of certain Leguminous trees, *Sindora* and *Afzelia* and of *Malvaceae*, *Neesia*. These arils are an evolution of the funicle into broad waxy processes, yellow in *Sindora* and *Neesia*, and red in *Afzelia cuanzensis*. The round 1-seeded pod of *Sindora* in most species is armed with spines exuding a gum at the tips, which may adhere to the foot of a large passing animal. The large basal waxy aril is undoubtedly destined to attract the rodents, and I have constantly found them showing distinct marks of rodents' teeth, or completely eaten away (Pl. XVI, fig. 8). In *Neesia*, the large woody Durian, the small seeds lying in the half-open capsule are furnished with a smaller waxy aril, often nibbled, and often completely eaten away. These fruits fall, when ripe, from the trees, which are from 60 to 100 feet tall, and the aril is attacked as they lie on the ground. These are both Malayan plants. *Afzelia cuanzensis* has a pod containing a number of

beans with a crimson waxy aril, and I have seen specimens of the fruit similarly gnawed, showing the marks of the small teeth of rodents. It is a big African tree. As these fallen fruits are only attacked by nocturnal rodents, I found it impossible to discover what species attacked the arils, but rats of many kind were very abundant in the Malay forests. The arils are evidently very popular with the rats, which often carry away the seeds with the aril. They sometimes, apparently, nibbled the seeds of the *Neesia* as well, but not those of the *Sindora.* I have eaten the arils of both plants and found them quite tasteless, much like very stiff wax. Troup mentions *Michelia excelsa* (*Magnoliaceae*) as having a red aril to the seed, which is also popular with, and sought for, by rats.

It is probable that many other of the bigger arillate seeds of the large forest trees are carried off by these animals. As a rule, seeds with coloured arils, especially pulpy ones, are destined for dispersal by birds, and I have therefore given the story of the aril under that subject (p. 423); but frequently, when the trees of *Myristica* and other trees bear a heavy crop, the ground beneath the forest is covered with fallen fruit, which is carried off by the rodents. They also probably carry off many of the hard-fleshed drupes fallen from lofty trees. The ground squirrels, which do not climb trees, must live entirely on fallen fruit, and of fruits not intended for dispersal in this way they must destroy great quantities. I have found, beneath a tree of *Shorea leprosula*, all, or almost all, of the crop of winged fruits lying on the ground gnawed into and destroyed. Rodents are often very destructive of seeds washed up by the sea on the shores, but the crabs are even more injurious in this way. However, the forest rats do aid in dissemination of some trees, the seeds of which, fallen from the high boughs, would never develop but for them.

In desert countries, where food is scarce, some of these rodents collect and store grain. Harding King (in " Mysteries of the Libyan Desert ") says that " desert rats (apparently meaning *Jerboas* or *Gerbilles*) store up grain and " travel long distances. He tracked one for 9 miles, and says that they can go as " much as 50 or 100 miles over the desert."

Cricetus frumentarius, the Hamster, stores seeds in holes and under rocks in abundance, and may be responsible for some amount of seed dissemination. The stores may be abandoned, some of the seeds dropped by the animal in conveying them, or the storer may perish or forget its hoard.

Arvicola sp.—S. Birger (in " Vegetations enstandiger Schwedischer Inseln," *Engler's Jahrbuch*, 38) says that a field vole carries to its nest portions of *Alopecurus agrestis*, *Gnaphalium uliginosum*, *Juncus articulatus* and *J. bufonius*, and *Polygonum lapathifolium*. Indeed, these voles carry about all kinds of grasses and other herbs, and may perhaps add to their dispersal to a small extent.

In South Africa Marloth says small rodents carry off and disperse the seeds of the Cycad *Encephalartos altensteinii.* " The seeds are drupe-like, bright orange " in colour, with an outer layer of integument and an inner one of pulp, beneath " which is a stony shell. This pulpy coat contains sugar, and attracts birds " as well as small rodents, which carry the seeds about and so disperse " them."

Porcupines (*Hystrix Africae-australis*).—Marloth says that in South Africa these animals, like baboons and jackals, dig up the underground fruits of *Hydnora Africana* and carry them off to eat in the shade of bushes.

Hare (*Lepus variabilis*).—According to Heinitz, the hare in Sweden feeds on the fruits of *Vaccinium* and *Pyrus aucuparia*.

Squirrels (*Sciuridae*).—These are the most important little tree-planters in the matter of oaks, chestnuts, beech nuts and walnuts, though they are also dispersers of other seeds.

In the Malay Peninsula the most common squirrels were the little *Nanosciurus exilis* and *Sciurus notatus*. They ate the green pericarp of such plants

as *Sideroxylon* (*Sapotaceae*), *Alangium Ridleyi* (*Cornaceae*), *Pyrenaria acuminata* (*Ternstroemiaceae*) and *Strombosia javanica* (*Olacineae*). These are all inconspicuous green fruits with a firm pericarp, and contain 1 seed in each, except the *Pyrenaria*, which resembles a small hard apple, and contains several seeds. It is common to find gnawed fruits lying some way from the trees, usually with the seeds uninjured. In many cases the tree is completely denuded of its fruits as soon as they are ripe, and the squirrels carry them so far away that it is impossible to find any. I have mentioned the devouring of the fruits of the Gingers *Nicolaia* under the account of rats, but it is quite probable that the squirrels are responsible for the destruction of this fruit as well as rats. They frequently also attack juicy fruits, and are especially destructive of the Chocolate pods (*Theobroma Cacao*) cultivated in gardens and plantations. These large red, green or yellow pods are borne on the trunk and thicker branches of the tree, and are attacked by the squirrels, which gnaw into the pods and extract the soft seeds enclosed in a sweet white pulp, which is the part they eat. They do not bite up the seeds, but throw them about. The Chocolate pod contains a considerable number of seeds, and, as it does not dehisce, the seeds would all germinate in one mass if the pod were not gnawed open and the seeds extracted and scattered by squirrels or some such animals. The tree is a native of the Amazons, and I have no information as to what animal disperses the seeds there. Monkeys and civets attack them in the East Indies as well as squirrels.

The Duku (*Lansium domesticum*) (*Meliaceae*), a favourite fruit in Malaya, is also eagerly attacked by squirrels. The fruits, about 1 inch through and globose, have a soft, leathery, pale buff pericarp, easily torn, which covers 3 or 4 soft green seeds enclosed in a pleasantly-flavoured white pulp. They hang in racemes from the trunk and thicker boughs of the tree, which is about 15 feet tall. The squirrels run off with these as soon as they are ripe, and eat the sweet pulp, pulling the fruit to bits. At one time we enclosed the ripening fruits in cloth bags to protect them, but the squirrels soon realised that the bags implied ripening fruit, and tore the cloth into holes to get at it. Wire-netting was often used to protect these fruits and chocolate fruits, but they pressed the wire down or got their noses through the interstices, and so bit into the fruits. The fruits of *Baccaurea Motleyana*, the Rambai (*Euphorbiaceae*), which resembles in appearance those of the Duku, but hang from the branches in longer strings, and have only 3 seeds in each, are equally attractive to the squirrels, and are eaten in the same way.

There are a considerable number of trees bearing this class of fruit in the Malay forests, i.e., with several seeds, often quite thin, covered with a sweet pulp enclosed in a soft indehiscent pericarp, which cannot be disseminated except in such a way by squirrels or some such mammal. They are dull and inconspicuously coloured, and usually borne on the branches of low trees, or on the stems, as in *Ryparosa* (*Flacourtiaceae*), *Baccaurea*, etc.

The fruits of the Rattans (*Calami*) are often eaten by squirrels. These climbing palms have oblong globose fruits covered with a yellow or brown scaly pericarp, quite thin. They contain 1 very hard round seed covered with a thin sweet pulp, which is nibbled by these animals, and the spiny stemless *Zalacca* has a large brown scaly fruit, containing 1 large stony seed in an acid pulp, which is also carried off by squirrels and rats.

The *Barringtonias* are small or medium-sized trees, usually occurring on sea-coasts or river banks, where the fruits, which are corky or pithy, containing 1 seed, are distributed by sea or river currents ; but several species occur far from water in the forests, and these are probably carried off by squirrels or perhaps rats. I have seen a squirrel run off with a seed of *Barringtonia racemosa*, usually a tidal-river plant, but in this case planted in the garden, and I have no doubt that the jungle species are disseminated in this way.

P. A. Buxton (in " Animal Life in Deserts ") quotes Spalding, who says that squirrels fatten on the fruit of *Echinocacti*.

Troup (" Sylviculture of Indian Trees ") states that Indian squirrels carry off fruits of *Terminalia belerica* (*Anacardiaceae*), *Lantana mixta*, *Corypha umbraculifera* and *Michelia excelsa*.

The English red squirrel, according to Heinitz, sometimes eats the berries of *Empetrum nigrum* in Sweden. C. B. Moffat (in the *Irish Naturalist*) says that in winter it sometimes eats the berries of the hawthorn, and also blackberries and bilberries, and occasionally indulges in a feast of yewberries, in Wexford.

But besides these firm-fleshed and juicy fruits which the squirrels eat, disseminating the seeds unhurt, they live largely, as is well known, on the seeds of *Cupuliferae* and the acorns of the Oaks *Quercus* and *Pasania*, the chestnuts of *Castanea* and *Castanopsis*, the seeds of the Beech (*Fagus*) and the nuts of *Corylus avellana* and other species, and although they actually destroy a large proportion of the seeds, yet they disseminate a sufficient number to actually benefit the species and ensure its propagation. In cold climates they effect this mainly through their habit of storing food for the winter ; but in tropical climates, where, if these trees are not actually fruiting all the year, and the supplies fall off, there is yet in the forests a sufficient supply of other fruits, as previously mentioned, as well as buds, birds' eggs or fungi, with all of which they supplement their food requirements, and, as far as I can ascertain, the tropical squirrels do not store food. There are in the Malay Peninsula a large number of Oaks (*Quercus* and *Pasania*), about 40 species, and Chestnuts (*Castanopsis*), 13 species. They are most abundant in the lowland forest, but some occur up to 5,000 feet altitude, and wherever they are found, squirrels are present. They fruit very heavily, more so, perhaps, than any other class of tree there, and the ground beneath an Oak in fruit is often covered with acorns, as, indeed, may often be seen in England, under the common Oak and *Quercus cerris*. Several species of the tropical Chestnuts (*Castanopsis*) have their fruits arranged in close spikes, and these spikes break off from the tree altogether, the separate fruits being non-detachable (*C. sumatrana*, *C. Hullettii*), and the cupules of most species are covered with sharp spines. A squirrel seizes a spike and breaks it off, and, holding it in its paws, attempts to nibble through the prickly husk to eat the fruit, and it often happens that, owing to the prickles being too sharp for its paws, it drops the whole spike before it has eaten more than one nut. Many of the species have more than one nut in the spiny cupule (generally 3), so that, if it takes off one of the cupules of a separate chestnut, it may only succeed in eating one of the 3 nuts before it drops the others. Even in the case of *C. sumatrana*, in which the spines are so blunt as not to be likely to hurt its paws, one often finds the spike, which is about 7 inches long and about 2 inches through, fallen beneath the tree, only partly gnawed, and still with good nuts in it. The squirrel invariably, after gathering a fruit or spike of fruits, runs off with it to some distance before it begins to eat it, so that the nut, or acorn in the case of oaks, may be dropped at some distance from the tree. If it drops the nut, it does not usually descend to pick it up, but goes and gets another.

I may here mention that my observations on the habits of Malayan squirrels were made, not only on the wild ones in the forest, but also on a number of species which I kept in captivity in the cages in the menagerie of the Botanic Gardens, Singapore, for some years, so that I was easily able to watch their various methods of dealing with acorns and chestnuts. The beautiful big squirrel *Ratufa bicolor* is an entirely arboreal species inhabiting dense forest, and never descending to the ground. When it takes an acorn or chestnut, it runs off to a suitable spot to devour it. It sits transversely on the bough,

holding on with its hind feet, and with its head and fore-paws hanging down on one side over the bough, and its tail on the other. In this position it is very likely to drop a chestnut (*Castanopsis*) too prickly, or an acorn which is too slippery, for it to grip firmly. The smaller squirrels, *Sciurus notatus* and *Nanosciurus exilis*, should they descend to the ground to pick up an acorn fallen from the tree, as they sometimes do, always runs up the trunk of another tree to eat it, and I have seen one carry an acorn many yards before it attempted to feed. I watched the small red-bellied squirrel, *Sciurus notatus*, eating the fruit of an *Elaeocarpus*. When it took a fruit it hung head downwards from a bough, holding on by its hind feet only, and of course dropping the seed when it had eaten the pulp. The little *Nanosciurus* usually hangs head downwards by its hind paws when eating an acorn, on the trunk of a tree, and the English Red Squirrel (*Sciurus vulgaris*) and the Grey Canadian Squirrel (*Sc. carolinianus*) often do the same. In some of the chestnuts, *Castanopsis Hullettii*, *C. sumatrana*, *C. nephelioides* and *C. Curtisii*, the cupules do not dehisce. The latter two are 1-seeded and are not spiny. The squirrel in eating these has to nibble through the rather thick cupule, and in so doing is very apt to drop it before it has got to the nut.

C. megacarpa has a very large oblong fruit, the solitary nut being oblong and 3 inches long. Its spiny cupule dehisces, and the nut is readily detached. A squirrel may eat a considerable portion of it before it injures it enough to prevent germination, but, as it is quite rounded, it appears to be more usually dispersed by rolling, or falling from its cupule.

The acorns of the Oaks are not covered with the cupule, except in one or two species, but are quite exposed, and though the cup is sometimes roughened with rather soft hooks (*Pasania hystrix*), they are not armed with spines, as in the chestnuts, but they have other aids to dispersal. If one examines the acorns which have fallen from a tree where there are many squirrels, one notices that they are all nibbled at the base, and that there are often marks of teeth as of ineffectual bites on the sides, showing that the little animals have attempted to eat them and accidentally let them drop.

I gave a *Ratufa bicolor*, which I had in a cage, some acorns of *Pasania lucida*, a large rounded acorn 1 inch through, hemispheric in shape, and with a thick, smooth, shining, polished mahogany-brown pericarp. It took the acorn in its paws and tried to bite the side of the nut, but the outer coat was so smooth that its teeth slipped, and it could not get a hold on it. It then turned the acorn round and bit the cup, and the acorn immediately fell out of the cup and rolled away. Had it been up in a tree when it tried to eat the acorn, the nut would have fallen down and perhaps rolled far away from the tree, and the squirrel would have had to content itself with the cup. I gave it the acorn again, and it was evident that the acorn was too slippery for its paws, and even on the floor of the cage it could hardly hold it firmly enough to eat it.

Many of the acorns have a rather firm outer coat thus polished and slippery, and fall very readily from the cup when ripe, but some, such as *Pasania encleisacarpa* and *P. Cantleyi* and *P. Wallichii*, all common species, have the acorn coated with very fine silky hairs, so that it has almost a greasy feel. It is not at all easy for the squirrel to grip it in its paws, and it is common to see the acorns of *P. encleisacarpa* scattered all over the wood when the tree is in fruit, and nearly all bear the marks of the squirrel's teeth, but are not injured sufficiently to prevent germination. This acorn has its cups in the form of a thin brown covering which, though cracked and split when the fruit is ripe, is never wholly detached.

In *P. Cantleyi* and other species the acorn is readily detached from its cup, and is very difficult for the squirrel to hold. It takes the acorn in its mouth by the raised rim at the bottom, and can carry it off in this way, but to eat it,

it must hold the slippery upper portion in its paws, so as to nibble at the base, the only part where its teeth can get a purchase, and it naturally lets many of them slip from its grasp unhurt to the ground.

Most of the tropical acorns have a much thicker coat than those of the English Oak, so that the squirrel has to nibble for some time before it reaches the cotyledons.

The amount of acorns produced by a tree is so large that the comparatively small number actually destroyed by the squirrels is negligible in proportion to the advantage to the species in getting the acorns dispersed throughout the forest. It is of course necessary for the tree to sacrifice enough of its acorns to tempt the squirrels. If the seeds were too well protected, so that the squirrels could never get at the kernels, they would not be likely to visit the trees at all. Indeed, where, as in the hill forests, there are few or no squirrels, there are not nearly so many oaks and chestnuts as there are in the lowland woods, where the squirrel abounds. The squirrels and oaks, in fact, go together, and where one is, the other will be found. In the forests of Berastagi, in Sumatra, at 5,000 feet altitude, I had not seen an oak or chestnut, till one day I saw a squirrel, and knew that one or other of these trees must be near, and, a short distance away, found both a *Pasania* and a *Castanopsis*, and their nibbled fruits lying beneath them.

Not all the squirrels of the Malay Peninsula feed on acorns and chestnuts. The flying squirrels *Petaurista* seem to feed mainly on fruits, often attacking coco-nuts, and Robinson and Kloss record *P. nitida*, in Bandon Island, as feeding on Durians. I have never seen any in oak or chestnut trees. Raffles' squirrel, *Sc. Prevosti*, also feeds on Durians and coco-nuts, boring into the nut on the Palm, and sometimes, after cleaning out the meat of the nut, making its nest inside; nor do the ground squirrels seem ever to eat the acorns or chestnuts, but probably feed mainly on fallen jungle fruits.

Storing Squirrels.—The English squirrel in the autumn collects acorns, nuts, or walnuts, and buries them an inch or two deep in the ground, sometimes several together, digging with its paws and pushing the nut into the ground with its nose, and then carefully covering it up. During the winter, if it is fine, it goes to the hiding-place and takes the food out to eat. It generally carries it to some distance from where it finds the nut. If storing walnuts, it often leaves the fruit buried till the unpleasant outer pericarp is decayed, and then digs it up to eat. At Bradbourne, near Malling, Kent, a squirrel was seen to run down from a walnut tree with a nut and bury it beneath the shade of a cedar tree. Some time later it was seen to go to the spot and take up the nut, of which the outer coat had decayed away, and eat it. Close to this spot are 3 young walnut trees evidently planted by this squirrel. They are 46 yards from the tree from which the fruit was derived. The squirrel who planted them had long disappeared.

In some cases the squirrel seems to forget exactly where it planted its stores, or is frightened away from the spot, or perhaps is dead, and thus this persecuted little animal plants the oaks, chestnuts, hazel-nuts and walnuts about the woods.

Mr. O. Pickard-Cambridge, in a note on the habits of English squirrels (in "Dorset Nat. Hist. and Antiqu. Field Club," vol. xi, p. 26, 1890) writes a good account of their behaviour thus:—

"I have observed them (squirrels), for many past years, busily engaged in "picking up acorns and burying them singly over considerable spaces of ground "in the immediate neighbourhood of the supply. There stands on my lawn "a large Turkey Oak, on which there are in some seasons, very large crops. "As soon as the acorns begin to drop (about the beginning of October), "several squirrels are at their daily work, beginning early in the morning and

"continuing at intervals all day. The space immediately under the tree is "searched carefully, and even though the acorns may be lying thickly on the "ground, yet it might appear to the observer as though there were some "difficulty in finding them, for there is a good deal of discrimination and "discretion exercised before one is taken in the mouth and conveyed rapidly "to a short distance from the tree. As soon as the burying ground is reached, "a little hopping about and sniffing among the grass reveal the proper spot, "where a small hole is scratched with the fore-paws, and the acorn is thrust "in with one or two pokes with the mouth, and still more hastily covered with "earth by a scratch or two. The squirrel then returns equally expeditiously "to the source of the supply. I have never seen the squirrels inter the acorns "beneath the tree, i.e., not within the distance of its spreading boughs. They "are often carried as far as 30 yards, though the bulk will be buried within "that distance." The writer attributes this to the instinct of animals, feeding together on fruit, to carry off food to some distance (certainly among some animals, e.g., monkeys and fruit-bats, there is a risk of a companion plundering another, which is a cause of their flight to a distance; I have, however, never seen a squirrel dispute the possession of a nut with a companion), but he points out that this carrying off of the acorns preserves the buried stores from the search persistently carried on by birds during the autumn and early winter. They would find every acorn if buried just beneath the surface under the tree, but there is no inducement to search for them farther away. Mr. Pickard-Cambridge goes on:—"The squirrels are often destroyed as vermin in the "autumn, but one or two manage to escape, and disinter the acorns in winter "and early spring. One year in particular, when none lived to find the acorns, "a curious result happened. For 3 weeks or a month at midsummer the lawn "had been left unmown, and among the long grass there had sprung up a fine "crop of Turkey Oaks, pretty regularly and thickly over the whole lawn." That squirrels are very critical of the nuts they carry off is certain, and the grey squirrels frequently reject nuts offered them. They probably know by the weight whether the kernel inside is good and will keep.

The Grey Squirrel of Canada (*Sciurus carolinianus*), now introduced into England, and spreading rapidly all over the country, has replaced the red squirrel in many places, and is as energetic a tree-planter as the red one, and perhaps even more so. It buries acorns, chestnuts, beech mast, hazel-nuts, and walnuts, also pine seeds. I have seen it carry off and plant seed of *Pinus contorta* in Kew Gardens. The whole of the shrubberies at Kew are now dotted all over with seedling oaks of various kinds, and beeches, usually under the shadow of bushes, through which they grow up, and these at a considerable distance apart, and some way from the original parent tree. I have seen a squirrel carry an acorn 80 yards from the tree and plant it. In some cases at Kew the acorns have been planted by jays, but far the greater number are clearly the work of the grey squirrel. Being in many parts of England much more abundant and bold than the red squirrel was even 50 years ago, it is really a much more important and effective planter than the latter ever was. It is commonly supposed that it drove out the red squirrel, but that animal was much persecuted by gamekeepers 50 years ago, and I think there is every reason to believe that its diminution in numbers was really due to an epidemic disease.

Squirrels also play a part in the dissemination of the seeds of the Pine trees, and seem to be especially important in dispersing those of the Pines whose cones do not dehisce, the section of *Cembrae*. In *P. koraiensis*, *P. cembra* and *P. albicaulis*, the seeds are wingless and the cones open. They are carried off from the trees by squirrels and mice, and also by Nutcracker Cows (*Nucifraga*). These animals break up the cones to eat the seeds, but in so doing

many escape unhurt, and in this way these Pines are disseminated (Prentiss, *Bot. Gaz.*, xiii, 1888, 326). *P. cembra* is a native of Europe, and is doubtless dispersed by the red squirrel. *P. albicaulis*, a native of British Columbia, is known also to be dispersed by squirrels. In the *flexiles* group of Pines the seeds are also wingless, but the cones open and release the seeds. These are probably dispersed by storing squirrels, as I have seen those of *P. contorta* carried off and buried by the Canadian squirrel in Kew Gardens, as already mentioned.

Hofman (in *Ecology*, I, p. 49) gives an account of the regenerating forests of the Douglas Fir (*Pseudotsuga taxifolia*) in America, in which he points out the importance of the storing rodents. He says the seeds of this fir and those of *Pinus ponderosa* and *P. monticola* are the favourite food of rodents, and when there is a large crop, they hide them in batches of from a few to a bushel of seed. Before spring, all traces of these stores are hidden by the action of snow and rain. These seeds will remain underground in a good condition for as long as 6 years. When the forest is destroyed by fire or by felling, these seeds germinate, and regenerate the forests. Such forests are found to consist of 75 per cent. of Douglas Fir and *Pinus monticola*, the most favoured seeds of the rodents. These facts show clearly the importance of the action of these animals. Though in this class of plants the rodents destroy by eating as many as they can manage, the excess of seed produced by the trees is their protection from extermination of the species.

In other countries, where droughts may occur, the squirrels also store provisions. J. D. Hooker (in the *Himalayan Journals*, vol. ii) writes that:—
" At Sonepore, in India, squirrels abounded and were laying up their stores.
" Descending from the trees, they scoured across a road to a field of tares,
" mounted the hedge and took an observation, foraged, and returned up the
" trees with their booty." This took place in February, and the squirrels must have been storing some Leguminous seeds against the long dry period in March.

Eutamias, the Chipmunks of North America, store fruits and seeds for the winter to a large extent. They generally collect and hide them in large numbers together, in crevices of rocks or beneath stones, or even in hollow trunks and branches of trees. This is not as satisfactory, from a dispersal point of view, as the habit of storing single fruits or two or three together in one spot, as the English and Canadian squirrels do, but many may roll away or be dropped by the animal while collecting, or may fall into crevices in the rocks, where they cannot recover them, and, having been transported to some distance from the tree or shrub, may in some such ways derive advantages of dissemination from the action of these chipmunks. As has been mentioned, other rodents store seed or grain in bulk. Rats, too, often carry off food of this nature to be eaten at leisure, without intending to actually store for a hard spell of winter. I have often found seeds and fruits collected beneath the shadow of rocks in Christmas Island and elsewhere, apparently brought by some rodent for present consumption. This plan of carrying off a number of fruits or seeds from a tree or shrub, to eat later undisturbed by competitors, may very well be the origin of the storing habit for winter or drought, which is so characteristic of rodents. Merrit Carey (in Biological Survey of Colorado, *U.S.A. Dept. Agric. Biol.*, 33) gives an account of the food and habits of the little Chipmunks (*Eutamias*) and the Ground Squirrels (*Citellus*). *Eutamias quadrivittata* eats the fruits of *Cercocarpus parvifolius* (*Rosaceae*), *Opuntia*, Juniper, Currants, wild Cherries and June Berries (*Amelanchier*). *E. hopiensis* feeds exclusively on the fruits of *Juniperus monosperma*, and *E. dorsalis* also feeds on Juniper fruits.

E. minimus eats Buffalo berries *Elaeagnus argenteus*, which it collects and

stores, as it does also fruits of *Sarcobatus vermicularis* (*Chenopodiaceae*), *Cleome* (*Peritome*) *Sonorae*, and *Symphoricarpus oreophilus*.

Citellus variegatus, the Rock Squirrel, feeds on Pine nuts, acorns, and seeds of apricots and melons. It carries the seeds among the rocks to be eaten at leisure.

C. columbianus, the Californian Ground Squirrel.—An account of the storing habits of this animal is given by W. T. Shaw (in *American Naturalist*, lx, 367) who records a list of the seeds found stored by it for the winter. He found in their caches grains of wheat, oat, barley, seed of apple, *Collinsia tenella*, *Alyssum alyssoides*, *Rosa Nutkiana*, *Bromus* sp., *Polygonum convolvulus*, *Rumex sp.* and bulbs of *Allium acuminatum*, *Erythronium grandiflorum* and *Zygadenus venenosus* (*Liliaceae*), a poisonous plant.

The dispersal of bulbs by mammals is unusual, though I know that some of the mice are very destructive to crocus bulbs, and may carry them off and drop them. Dr. Dallátorre describes a method in which crocus bulbs were dispersed in Austria by moles. He found hundreds of bulbs of *Crocus albiflorus* thrown up on mole-heaps by the digging of these animals. These heaps were later spread over the fields by rain-wash, and the bulbs were diffused by the rush of water, besides which dogs digging in the mole-heaps scattered the bulbs about. This, it must be admitted, is rather a feeble dispersal method, but may account for the distribution of crocus or other bulbs over a field or hillside.

Marsupialia.—I have very little information to offer on the dispersal of seeds by marsupials, though some of the vegetable feeders must take some part in this work. It is recorded, however, that the Opossums, *Trichosurus vulpecula* and *T. fuliginosa* and *Phalangista vulpina*, were introduced into New Zealand from Australia, and, though feeding mainly on leaves and buds of trees, also ate the fruits of *Griselinia*, *Panax*, *Pittosporum*, *Rhipogonum*, *Fuchsia* and *Aristotelia*. Most at least of these fruits, however, have their seeds more satisfactorily distributed by birds.

Wallabies are recorded (by Alexander) as distributing *Opuntias* (p. 365).

CHAPTER IV

DISPERSAL BY BIRDS

FOREWORD: BIRDS AND THEIR FOOD.

IN this section I record such evidence as I possess as to what fruits and seeds are swallowed by birds, and of which the seeds are evacuated in a fit condition for germination; but although we know to a large extent the food of the food-eating birds in Europe and North America, observers and recorders of this subject in the tropical regions of Asia, South America, and Africa have been very few in number.

The ordinary ornithologist is not, as a rule, sufficiently conversant with botany to say what kind of a fruit he sees a bird feeding on, or what kind of seed it has in its crop when opened, while the botanists seldom make any observations on the birds which they see devouring seed, as they do not know what kinds of birds they are, so that a good deal of research and investigation on this subject is thus required.

It does not follow that, in all cases in which a bird is found to contain seed in its crop, the seeds will pass through the intestine and be evacuated in a germinable condition, but it does occasionally happen that when seeds swallowed by a granivorous bird, or by one of the seed-crushing finches (which usually destroy them during digestion) are eaten in very large quantities, some do pass through the bird quite uninjured. The finches are often accredited by agriculturalists with the destruction of noxious weeds. Such seeds as those of Charlock, having no pulp or aril from which the birds obtain nutriment, are normally crushed or digested when swallowed, as it is the albumen and cotyledons of the seeds on which they depend for nutrition, but it is clear that occasionally some of the seeds do pass through the bird undigested, especially if they are abundant, and the bird can readily gorge itself with them. Again, in carrying off the seed, the birds occasionally accidentally drop them, often at some distance from the mother-plant, and while feeding or returning from the feeding-ground with a full crop, are often surprised and taken by hawks or other birds of prey, and torn to bits, the contents of the crop being strewn about the ground and so dispersed. The most satisfactory evidence of actual dispersal is the finding of the uninjured seed in the excreta, and the occurrence of plants with berries or drupes in or about the bird-roosts, or of isolated ones of such a nature, at a distance from the parent plants, at spots haunted by frugivorous birds.

When a bird finds a large supply of fruits, drupes or berries, and gorges itself therewith, it frequently regurgitates the seeds in pellets or loose masses, at some distance from the parent tree. This is commonly done where the seeds are large, as in cherries, or where the fruits grow in masses, as in the case of the Rowan Tree (*Pyrus aucuparia*), or the heavily-fruiting *Cotoneasters* and *Pyracanthus*, while in the more scattered fruits, as of the holly, the seeds are commonly swallowed and passed in the excreta. In feeding the nestlings

also, I believe that the bird transfers only the pulp of the fruit to the young ones, expectorating the stones or hard seeds near the nest.

The size of the seed swallowed by a bird naturally depends on the size of the bird. Large birds do not, as a rule, swallow very small drupes and berries when they can find larger ones, and small birds usually neglect large-sized ones, or bite off the pulp only in large drupes. In large fruits, like those of *Fagraea imperialis* or the *Papaya*, the small birds eat the pulp, carrying with it the small seeds. The size of some seeds swallowed by such birds as the fruit-pigeons and the hornbills is very large for the size of the bird's intestine; but in many instances the large seeds are not, in this case, passed through the intestine, but disgorged after the pulp or aril has been detached in the crop. However, the large seed of the nutmeg is transported to a considerable distance over sea by fruit-pigeons, and apparently passed through the bird. Still, plants possessing very large seed of this type are always absent from distant oceanic islands.

To show the important part played by birds in dissemination of plants, I published (in the *Natural Science*, viii, 197) some lists of plants found on or at the foot of various trees in the Singapore Botanic Gardens, which I republish here.

Oil-palms, date-palms, sago, and other palms retain on their stems in the axils of the fallen leaves (of which the projecting bases remain for many years) a quantity of soil, partly blown there by wind, and partly formed of decaying pieces of leaf-bases, but even more largely of soil carried there by ants, who make their nests there. These pockets of soil form suitable spots for the growth of many plants, especially epiphytic ones. Birds roost in these Palms at night, and often sit there by day, and frequently evacuate there the seeds of fruits which they have eaten, and the smaller fruit-bats also frequently fly there and deposit seeds. I recorded the following plants found growing on some of these plants :—

A. On an oil-palm (*Elaeis guineensis*) :—

Rhodamnia trinervia.—A tree with small black berries, much eaten by the common Bulbul (*Otocampsa analis*).

Ficus urophylla.—A shrubby plant with orange figs, eaten by birds, commonly epiphytic.

Ficus polysyce.—A tree, figs green or purplish-red, largely eaten by fruit-bats.

B. An oil-palm :—

Clidemia hirta.—Terrestrial herb. Berries black, eaten by many birds.

Cyrtophyllum fragrans.—Tree. Berry orange, eaten by birds.

Ficus rhododendrifolia.—Figs black, eaten by birds, and many ferns, the spores brought by wind.

C. An oil-palm :—

Clidemia hirta, *Ficus* sp.; and *Phyllanthus niruri*, a small herb, the seeds of this probably brought by ants.

D. Date-palm (*Phoenix dactylifera*) :—

Ficus urophylla, *Phyllanthus urinaria* (probably brought by ants); many ferns, and *Psilotum*, brought by wind.

E. *Livistona chinensis* :—

Ficus urophylla; *Fagraea imperialis*, a shrub growing near, with dehiscent fruit bearing many small seeds in a sweet orange pulp, eaten by birds; this is at first epiphytic, finally killing its host and becoming a large shrub or tree.

The greater part of this tree-flora is thus composed of bird-disseminated plants with coloured berries or figs. The date-palm, with its thick head of stiff pungent leaves, was not well suited for birds to roost in, and much exposed to wind, hence the preponderance of wind-dispersed cryptogams.

Besides roosting on trees at night, birds have a habit of frequenting bushes, and often drop seeds round the buttressed trunks of trees, or on the ground from the branches. The excreta, dropped on branches, railings, and such places, are washed to the ground by rain, when the seeds then germinate. Thus around isolated trees, thickets are often formed by bird-borne seed evacuated on the branches. This vegetative growth induces more birds to come, at first for a shelter or a resting-place, and later to feed on the fruit of the trees or bushes they have previously brought. The thickets, ever being added to by the birds, develop into woods, and the country becomes soon afforested.

In the Malay Peninsula the long thick grass known as Lalang (*Imperata cylindrica*) covered great areas at one time, the result of felling and burning the forest. In time, if protected from further fires, the area would be seen to be scattered with small bushes of *Melastoma*, the fruit of which, pulpy black with small seeds, is very popular with Bulbuls (*Otocompsa analis*), and often with bushes of *Lantana*. Then come numerous bird- and bat-dispersed plants, *Macaranga*, *Cinnamomum*, *Adinandra*, *Morinda*, *Premna* and *Ficus*. All these together shade out the grass and make secondary jungle (known as Belukar), and gradually, if the forest is near enough, plants with winged fruits, and more bird-dispersed trees and shrubs come, and the area is once again covered with high forest.

The part thus played by birds, and I may add fruit-bats, in reafforesting land ruined temporarily by man is of great importance, as they commence the work of reclothing the ground with woody plants.

Development of thickets and woods may be seen in action in many parts of the Downs in England. I have mentioned already that on the Dorsetshire Downs, where gorse bushes are burnt so as to be reduced to bare branches on which birds do not roost, one finds only wind-dispersed plants coming up, while in and around leafy bushes the plants growing are those with drupes or berries, such as *Crataegus*, *Hedera*, *Solanum dulcamara*, *Rubus*, *Rosa*, *Sambucus*, *Lonicera*, *Ilex*, *Taxus*, and sometimes *Rhamnus*, *Cornus* and *Prunus*, disseminated by birds. The same evolution of woods and thickets round trees, due to birds, is also to be found in all warm regions.

B. D. Burtt, in a report on the dispersal of seed by animals and birds in Africa, dealing with the Tanganyika Province, writes :—" A particularly " striking case of the important factor that birds are, in the dispersal of the " seeds of the thicket *Grewia* (*G. Holstii*), was seen at Matabele, where turtle- " doves and bulbuls came to water at an open well. Above the well was a " young *Acacia verugera* tree that was used by the birds as a resting and alighting " place prior to drinking. The ground below the tree was covered with the " seed of this *Grewia*, dropped by the birds in their dung. The area was " estimated to measure approximately 250 square feet, and it was estimated " that some 550,000 seeds of the *Grewia* lay beneath the tree, the nearest thicket " of it lying over ¼ of a mile away."

I examined the plants springing up round and beneath some of the trees and bushes in the Botanic Gardens at Singapore, places where birds roosted at night, or sat in the heat of the day, and recorded the plants found there, which proved very instructive.

(1) A very lofty tree, *Terminalia subspathulata*, about 150 feet tall, with stout buttresses, had a big woody climber, *Spatholobus ferrugineus*, clinging round it to the very top. Birds used often to roost here, and, by bringing seeds, formed quite a thicket of shrubs between the horizontal base of the liane

and the buttresses of the tree. Monkeys and squirrels also often visited it. Among the shrubs and small trees here, were the following:—*Flacourtia cataphracta*, the *Rukam*, a small tree with dull purple fruit as big as a marble, very juicy, with several seeds, and popular with birds; *Erycibe Princei* (*Convolvulaceae*), a climber with dark red, almost black berries; *Passiflora laurifolia*, a climber, a large yellow many-seeded fruit, the seeds covered with a sweet pulp, eaten by birds, fruit-bats and monkeys; *Pithecolobium lobatum* (*Leguminosae*), a tree, the seeds of which are carried about by squirrels; *Fibraurea chloroleuca* (*Menispermaceae*), a climber, drupes orange-yellow, seeds transported by civet-cats, also by birds. *Clerodendron disparifolium* (*Verbenaceae*), tree, berry black, surrounded by a red calyx, eaten by birds; *Scleropyrum Ridleyi* (*Thymeleaceae*), shrub, fruit fleshy, pear-shaped, with a large round seed (perhaps dispersed by monkeys; I did not know of another plant within 10 miles); *Agrostistachys longifolia* (*Euphorbiaceae*), low shrub, capsule explosive; common in woods near by.

(2) An equally large *Shorea leprosula* tree close to the *Terminalia*. At its base were:—*Pithecolobium lobatum* and *Passiflora laurifolia*; and *Cupania pallidula*, a small tree with red capsules and black seed with a red aril, much sought after by birds.

(3) A large bush of *Bougainvillea spectabilis*, a favourite resort of birds, contained:—*Embelia garciniaefolia* (*Myrsineae*), with small red drupes, popular with birds; *Vitis hastata*, a vine with black grapes; and *Clidemia hirta*, with black berries.

(4) A much-branched Fig tree (*Ficus*), standing alone on the lawn, sheltered beneath its stems many plants, some of which were fairly large trees:—*Eugenia Jambos* and *E. grandis*, *Calophyllum inophyllum*, all generally disseminated by fruit-bats, which often roosted in the tree; *Flacourtia cataphracta*, several plants; *Cinnamomum iners*, drupe black; *Quassia amara*, fruit black; *Gomphia oblongifolia* (*Ochnaceae*), drupes black on a red disc; *Cupania pallidula*; *Lantana mixta*, drupes small, black; and *Caryota mitis*, with black drupes; *Arthrophyllum ovalifolium* (*Araliaceae*), a tree with green or blackish fruits; *Rhodamnia trinervia*; *Ilex cymosa*, tree with small red drupes; *Olea maritima*, a bush with small black drupes; *Thunbergia laurifolia*, and *Ruellia repens* (*Acanthaceae*), the latter, occurring near by in the grass, have explosive capsules.

All these plants occurred in the Gardens, but most of them within a radius of 100 yards or so. It is in this way that from isolated trees or bushes a thicket may spring up in a very short time round the tree or through the bush, and as the thickets increase in size and become the roosting-place of more birds, copses may be formed, then more extensive woods, and finally forests.

In a very valuable paper published in the Bulletin No. 261 of the United States Department of Agriculture (1918), Mr. E. R. Kalmbach gives an account of the common Crow and its relation to man. The crow dealt with is *Corvus brachyrhynchos*, which is extremely abundant in North America. This bird, which is a great fruit-eater, does not swallow the seeds of the fruits it devours, but, after assimilating the pulp, disgorges the seeds in pellets, as owls and kestrels do the bones of the mice they eat, and as in many cases our blackbirds also do with hard fruit-seeds, when fruit is eaten in quantity. The crows disgorge these pellets very extensively at their roosts. These roosts are chiefly established in the cold months—from September to March. They are usually formed in trees, though the crows have also been known to collect in low vegetation, such as reeds or tall grass, and in some cases even, in severe weather, on the ground in open fields or on exposed sand bars. Here two points may be noticed: one that the time of formation of the roosts, i.e., the flocking together of the birds, is that of the period when fruits are most abundant;

and secondly, that the birds do occasionally roost in open spaces very suitable for the growth of vegetation brought by them in the form of seed.

The number of crows collected at one of these roosts varies from 70,000 to 270,000 birds. Prof. Barrows visited a crow-roost on the Botanic River, just opposite Washington, in 1889. It covered an area of 12 or 15 acres of second growth deciduous trees. The ground beneath the trees was covered with an almost even layer of the ejecta of the crows, probably in most parts less than ½ inch, but in some places 1 inch thick. All the material from above the leaves from an area 2 feet square was collected and examined. When dry, it weighed almost exactly 1 pound, and of seeds contained :—

Rhus toxicodendron	1,041 seeds.
Rhus venenata	341 ,,
Other species of *Rhus*	3,271 ,,
Juniperus virginiana	95 ,,
Cornus florida	10 ,,
Nyssa sylvatica	6 ,,
	4,764 ,,

Thus, as Prof. Barrow points out, the roost of 15 acres must have contained upwards of 778 million seeds.

In other pellets Mr. Kalmbach found, besides the seeds of *Rhus*—apparently the most popular fruit with crows—those of grapes, *Vitis*, *Celtis*, *Strophostyles* (*Phaseolus*), *Bumelia* and *Smilax*, and many other seeds were also found in the stomachs of the crows.

It is pointed out in this paper that in most of the roosts in dense pine forests and such spots the seeds would not find a suitable locality for growth, but it is certain that the crows discharge their pellets not only at the roosts, but here and there over the birds' feeding range. The seeds would, no doubt, also grow on the outer edges of the roost-forests, and some would be washed out to some little distance from the shade of the forests by rain, into more or less suitable spots for growth. The occurrence of the dry bean (*Strophostyles* or *Phaseolus*) in the pellets is interesting as showing how dry seeds may be transported by birds.

I have examined the adventitious flora beneath the largest Horse-chestnut tree in Kew Gardens, which is surrounded by an iron railing, so as to obtain an idea of the proportions of plants whose seeds were brought by birds and in other ways. I find the following flowering plants in the enclosure, which is surrounded by a wide grassy plot :—

Bird-borne :—

Viburnum lantana, nearest bush 70 yards away; *Crataegus oxyacantha*, *Rubus fruticosus*, *Hedera helix*, *Ilex europaeus*, *Sambucus nigra*, *Prunus cerasus*, *Taxus baccata*.

Brought by squirrels :—

Two or three species of Oak, *Quercus*.

Wind-borne :—

Fraxinus excelsior, *Taraxacum Dens-leonis*, *Poa annua*, *P. pratensis*, *Dactylis glomerata*, *Epilobium angustifolium*, *Rumex acetosa* and *Rumex* sp. *Acer pseudoplatanus*.

Dubious, brought either by wind or rain-wash :—

Ranunculus repens, *Urtica dioica* (possibly brought adhering to a bird) *Digitalis purpurea*.

It was noticeable that the bird-borne plants were in many cases close to the railing, as if the bird had evacuated on it, and the seeds washed to the ground

below. These were *Prunus*, *Viburnum*, *Ilex*, and some of the *Sambucus*. Possibly the 3 grasses had migrated from the grass plot by creeping stems, but more probably from wind-drifted grain.

A good account of the dispersal of Orange trees and Allspice or Pimenta trees by birds is given by Morris (in *Nature*, xxxv, 151, and xxxvii, p. 466). He says, up till lately (he is writing in 1887–1888) very few orange trees were planted in Jamaica, and that nearly all the trees were planted by birds. This, indeed, anyone visiting Jamaica might guess, noting that the trees of the orange and other citrus fruits are scattered all over the country, in places where they were most unlikely to have been intentionally planted. Gosse (in the "Birds of Jamaica") records *Icterus leucopteryx*, a hang-nest, and *Turtur leucopterys*, a turtle-dove, as feeding on the oranges. Amadeo (*Nature*, xxxviii, p. 535) confirms Morris's statement above also as regards Porto Rico.

Morris (l.c.) quotes (from Lunan's "Hortus Jamaicensis," ii, 67), where he says :—"The usual method of forming a new Pimento plantation is to "appropriate a piece of woodland near an already existing plantation. In "twelve months after the rains, abundance of seedlings will be found growing "vigorously from seeds scattered by the birds. Birds eagerly devour the ripe "seeds, and, muting them, propagate the plants in all parts of the woods. It "is thought that the seeds passing through the birds undergo some fermenta- "tion which fits them better for vegetation than those gathered from the "tree." Morris himself adds that the present plan of forming plantations in Jamaica is exactly as described above. All the present plantations in Jamaica have been formed by frugivorous birds. The birds described by Gosse as feeding on the Pimento are *Myriadestes armillata*, *Conurus flaviventris* (a parrot), *Icterus leucopteryx*, and *Columba leucocephala*.

The Pimento or Allspice (*Eugenia pimenta*) is a bushy tree from 20 to 30 feet tall, with deep green leaves and panicles of black or purple 1-sided fruits about as large as a pea, from $\frac{1}{5}$ to $\frac{3}{10}$ of an inch through. The tree is a native of Mexico, Costa Rica, Venezuela and the West Indies. The seed requires to be well washed to free it of the pulp before sowing it, as the pulp becomes hard and dry and prevents germination. This is effected by the birds, which swallow it and pass the seed clean of pulp. It is well known that seeds of drupes will not germinate as long as there is any quantity of the pulp left attached to them, and their germination may be retarded a year, or altogether prevented, if the seeds are not thoroughly cleaned of pulp. It is noticeable that the unripe fruit of the Pimento is more strongly aromatic than the ripe fruit, so that for spice it is gathered young. It is quite probable that the birds dislike the aromatic spiciness, and its excess in the young fruit may act as a deterrent, preventing the bird from eating it until it is ripe, somewhat analagous to the conditions of the fruits of the *Alpinias* (*Scitamineae*) of the *Catimbium* section. These *Alpinias* have globose capsules of a conspicuous red or orange colour, which partially dehisce, and exhibit numerous very aromatic black-angled seeds enclosed in a white sweet non-aromatic aril. The birds, swallowing the seeds for the sake of the sweet pulp of the aril, do not crush the seeds, probably disliking the spicy taste.

That some birds do like a spicy flavour is shown by the popularity of the aromatic aril of the nutmeg, much sought after by fruit-pigeons, but the greater number of the arils of the other species of *Myristica* are not at all spicy, being nearly tasteless, and these seem quite as popular with birds. The banana-like pod of Vanilla is sweet, but not aromatic when ripe; the aroma only appears when the fruit is dried off, long after it has ceased to be fit for eating by birds or mammals.

However, birds often eat and distribute pungent fruits or even some that are bitter and poisonous to man. *Capsicums*, especially *C. minimum*, the Bird Pepper, is very popular with birds, which disseminate it plentifully over lime-

stone rocks. Most, if not all, of the fruits of the species of *Strychnos* are eaten by monkeys and civets, and the small yellow-fruited ones by birds. The inconspicuous small and very poisonous fruits of *Sapium sceleratum*, of Fernando de Noronha, were eaten and disseminated by small birds. *Datura* seeds are said to be eaten by goats, and there can be little doubt by birds also, otherwise it is difficult to account for its appearance in Christmas Island. Among plants poisonous to us, but of which the fruits or seeds are eaten by birds, are :—*Euonymus europaeus*, *Rhamnus catharticus*, *Bryonia alba*, *Atropa belladonna*, *Solanums*, *Daphne laureola* and *D. Mezereon*, *Arum maculatum*, and *Tamus communis*. *Adenia*, popular with birds in the Malay region, is said by the Malays to be poisonous, as is *Trichosanthes*. My hornbill, after swallowing an *Areca* fruit, disgorged the seed, which is poisonous to some extent, and birds frequently disgorge, or do not swallow, the seed of the nutmeg (*Myristica moschata*). This is possibly due to the size of the seed as much as to its poisonous or aromatic qualities. I may here note that few of the wild nutmegs are really aromatic, besides *M. moschata*—*M. fatua* and *M. cinnamomea* are the only *Myristicaceae* I know which have any aroma, and that but slight.

PART I

ATTRACTION BY COLOUR

Colours—Red Fruits—Yellow Fruits—Pink Fruits—Brown-purple Fruits—Black Berries and Drupes—White Fruits—Blue Fruits and Seeds—Fruit Coloration and Foliage—Mixed Coloured Fruits—Coloured Panicle or Cyme Branches.

THE fruits which are adapted for the attraction of birds are almost invariably brightly and conspicuously coloured, so that they are visible for a considerable distance against the background of green foliage by which, in a normal state, they are surrounded. Small berries are usually produced in panicles or cymes, so that the mass of colour can be easily seen at a distance, and it is noticeable that, in the case of such a tree as the Rowan tree, when the masses of berries have been cleared off by birds, isolated fruits or small bunches, hardly conspicuous among the leaves, are entirely neglected, and remain on the trees till they decay and fall off.

I have pointed out that fruits specially adapted for the food of mammals are not coloured, but dull, plain green or blackish. There are, however, cases in which birds seek out and devour uncoloured fruits, and many such fruits, especially *Ficus*, *Sapotaceae*, etc., are eaten and their seeds dispersed both by mammals and birds. The White Mulberry (*Morus alba*) is very popular with birds, but its fruits are very inconspicuous, and cannot be seen at any great distance. As every observer of birds knows, the sight of one or more birds feeding will call the attention of all the others for a long way round, whether it be vultures at a carcass or sea-gulls at a shoal of fish, and should a bird be seen obviously feeding on a fruit tree, other frugivorous birds flock there at once.

The bright red and orange colour of the fruit is an intimation to the bird that it is ripe, the full colouring not appearing till the seed is ready for dispersal. In many cases the juiciness and sweetness are an important asset. The sweet juicy Rowan tree berries disappear as soon as the fruit is red, while the equally conspicuous but firmer-textured and drier fruit of the *Pyracantha*, and the acid berries of the Barberry and *Hippophae*, remain long untouched on their bushes, showing that they are less popular.

The colouring in drupes or berries lies usually in the ripened pericarp, or (in the case of flowers with an inferior ovary) in the calyx-tube which is closely adnate to the ovary. In capsular fruits the conspicuous part is usually the soft, swollen outer part of the testa of the seed, or an aril which covers or partly covers the seed or is merely attached at the base. This is the part of the fruit eaten off or swallowed whole by the bird. When the seed is only partly covered by the aril, the testa of the seed is usually black, to contrast with the brilliant orange or red aril. If, as in some nutmegs, the seed is entirely covered by the aril (*Gymnacranthera Farquhariana*), the testa of the seed is light brown. In some cases the capsule is brightly coloured red, pink, or white, to contrast with the orange or red aril and the black seed. I call these TRI-COLOUR fruit; and those in which the seed is covered by the aril, and so has only two conspicuous colours, or in which the capsule is dull-coloured, and only the black seed and yellow aril are conspicuous, BI-COLOUR fruit. Arils are invariably red,

crimson, or more commonly orange-yellow, very seldom white, and never black or blue. The pulpy testa of the seed may be any of these colours.

Besides the external colouring of the fruit and the coloured aril or testa of the seed, there are other means of attracting birds in special cases. The genus *Melastoma* (*Melastomaceae*) comprises a considerable number of Asiatic bushes with showy mauve or white flowers, the ovary of which is inferior, and the calyx-tube, usually covered with scales or hairs, enclosing the ovary is of a dull inconspicuous pink (Pl. A, fig. 3). When ripe, the fruit splits across somewhat irregularly, or in one species, *M. schizocarpa*, vertically, and exposes the minute seeds imbedded in a sweet black pulpy mass, very attractive to pigeons, bulbuls, and other fruit-eating birds. These bushes occur in open country heaths and open woods, rarely deep forest. Here the septa and placentas, and not the pericarp, are the attraction to the birds, forming the black pulpy eatable part of the berry.

Some of the *Gardenias* (*Rubiaceae*), *G. tubifera*, a river-bank bush, and *G. resinifera*, a tree about 40 feet tall, have woody capsules of a dull green outside. They split irregularly, and the segments spread out, showing the placentas and lining of the pericarp to be of a bright orange or saffron colour, soft and sweet. In eating this, the birds swallow the small seeds, which they thus disperse. A similar arrangement occurs in *Fagraea auriculata*, mentioned on p. 420.

COLOURS.

The colours of fruit or seeds destined to attract the attention of birds are the following, arranged in order of frequency :—

Red or crimson ; yellow to orange ; black ; white ; blue, light azure to dark blue ; brown purple ; rose-pink.

In some cases we find 2 or even 3 colours combined in the infructescence, or fruit and seed, so as to set off each other. Thus in *Sterculia Jackiana* and other species, the carpels dehisce, spread out, and are of a brilliant scarlet, while from the edges depend the large blue-black seeds. In some *Pinangas* (Palms) the rachis of the inflorescence branches becomes a bright red, while the seeds are black. In the nutmeg, the mace (aril) is orange or crimson, forming a network over the black testa of the seed. In tricolour fruits we have three colours, thus : *Momordica charantia*, the pumpkin, is orange, it dehisces, and shows, inside, the black seeds with a crimson aril. In *Dysoxylon* the capsule is orange or red, and, dehiscing, exposes the black seeds half covered with an orange-coloured aril (Pl. XVI, figs. 3 and 4). In *Iguanura* and other palms the fruits are first white, then become red, and finally, when ripe, are black, and, as all do not ripen simultaneously, there are white, red and black fruits on the same spike. The birds eat only the ripe black fruits; the transition colours merely serve to set them off, or make the spike conspicuous from afar in the dark forests. Somewhat similar is the case of the Wayfaring tree (*Viburnum lantana*), in which the unripe fruits are scarlet, the ripe ones black and juicy; they ripen a few at a time, and the birds eat only the black fruits.

The plants which have coloured fruits are nearly all shrubs, climbers, or small-sized trees. The seeds of herbs are mainly dispersed by wind or rain, those of the lofty trees mainly by wind, rolling when fallen, or by mammals.

Fruits, when eaten by birds, are of comparatively small size, not more than $1\frac{1}{2}$ inches through, but fruits which dehisce and expose the seeds, provided usually with an aril or some amount of pulpy testa, may be of large size. In these cases the seeds only are removed by the birds.

Plants of the same order, genus, or species, may have fruits of different colours. Most of the plants of the low, half-shrubby *Labisia* (*Myrsineae*) have

red fruits. One, however, has blue. *Euthemis leucocarpa*, a low half-shrub, has conspicuous spikes of fruit, in some plants snow-white, in others rose-pink, in others bright red, all growing together. The Vines have black, white, yellow, or red fruits, according to species. The large genus *Eugenia* has fruits adapted for dispersal by mammals as well as by birds, and in the bird-dispersed species the fruits are of varied colour. I give a special note of it.

Eugenia (*Myrtaceae*), the Tree-Myrtles, a tropical genus of trees, more rarely bushes, and in one species only a climber, are very widely distributed over all tropical and subtropical regions. A very large number of species are described, upwards of 1,000, and they are about the most abundant trees in the tropical forests. They occur all over Africa, India, Malay regions, Cochin-China, China, Formosa, Australia, New Zealand, America from Florida southwards to Chile, and are found in many islands, Mauritius, Christmas Island, New Caledonia, Fiji, Tonga, Vavau, Hawaii and other Polynesian Islands, and South Trinidad.

The fruits are fleshy or pulpy and 1-seeded (rarely, accidentally, 2-seeded), and vary in size from that of a small pear to that of a pea. The animals which disseminate them are birds and fruit-bats, monkeys and civets. The large fruits are generally green or white, and are dispersed by the mammals. The small ones, which are usually to be found on small trees and bushes, are purple, black, white, red, or yellow, and are disseminated by birds; such are *Eugenia ugni*, of South America, a tall shrub, fruit red; *E. xanthocarpa*, bush, Ceylon, yellow; *E. braziliensis*, a low tree, black; *E. zeylanica*, small tree or bush, Malaya, white, pithy, and rather aromatic, very widely spread in open country from Ceylon over the Malay region; *E. acuminatissima*, a rather tall Malay tree, fruit dark violet-blue.

It is noticeable that the smaller fruits are more juicy and sweet, and conspicuously coloured, and grow usually on low trees or bushes, and obviously adapted for dissemination by birds, being especially sought for by pigeons. The fruits too big to be swallowed by birds, such as those of *E. grandis*, *E. javanica*, which are about 1 inch through, are inconspicuous, and green or whitish, with a firm fleshy pericarp, and these are disseminated by mammals, especially by fruit-bats.

The species which reach oceanic islands have small fruits easily transported by birds. The Christmas Island species was an immense tree with small purple fruits. One species recorded as *E. speciosa* L. reached Long Island, off Krakatau, by 1897, but I can find no species of that name described. It might, perhaps, be one of the large-fruited Jambosa section, and the seed transported by sea. In South Trinidad a species of the section *Syzygium* (small-fruited trees) has been collected, and the dead timber lying about on the island is said to be Myrtaceous and probably that of an *Eugenia*. This is interesting, as no frugivorous birds have been seen or collected on the island. But in most oceanic islands the genus is absent, e.g., Laccadives, Maldives, Fernando de Noronha, Juan Fernandez (though 2 species of *Myrtus* occur there), Cocos-Keeling Island, Galapagos.

Red Fruits.

By far the most conspicuous colour in Nature against the green foliage is red, which, if in mass, can be seen for a very long distance. Everyone who has visited the dense forests of the tropics knows how conspicuous a tuft of red flowers or fruit is against the walls of green along the tracks or river banks; consequently it is far the most common colour of fruits dispersed by birds.

It is not only an intimation to them that there is food waiting for them, but also that it is ripe.

Mr. Woodruffe-Peacock (in the *Selborne Mag.*, xxviii, p. 80) points out that blackbirds ate the fruit of red currants first and of black currants later, but not white or yellow ones, so that the red-fruited currant was the first dispersed. He observed this for many years, and the fact has been recorded by many other observers. His suggestion is that the birds thought the yellow and white fruit were not ripe. I notice also that the berries of the yellow-fruited holly are seldom, if ever, touched by blackbirds, and remain on the trees till they fall, while the red ones are regularly consumed if times are hard. I notice, too, that the black drupes of the Privet (*Ligustrum vulgare*) often remain untouched during the whole winter, long after all the red holly berries have been quite cleared off. The black ivy berries (*Hedera helix*) are not usually eaten till the nesting season, but the plant flowers very late in the year, about November, and the fruits are not thoroughly ripe till the young birds are hatched, and so are fed on them. The first fruits to be eaten by the birds in England are the sweet juicy berries of the Rowan tree (*Pyrus aucuparia*), the succulent juicy aril of the Yew (*Taxus baccata*), and the orange arillate seeds of the *Euonymus*. These disappear as quickly as they ripen, under the attacks of blackbirds, song-thrush and missel-thrush. The berries of the Rowan tree are produced in conspicuous panicles, visible for a considerable distance; those of the Yew stand out brilliantly against the deep green foliage; the *Euonymus* sheds all its leaves, so that the whole bush is conspicuous afar from the bright pink capsule and the orange-red or yellow seeds. The birds do not touch the fruit of the Rowan tree while it is still in the orange-yellow stage of ripening, except occasionally in a dry spell, when they eat the fruit as soon as it begins to change colour. The juiciness of the fruits in the autumn certainly appeals to birds, as the sweet pithy berries of *Pyracantha coccinea* are not eaten till later. In my garden the berries of a Rowan tree disappear long before those of an adjacent *Pyracantha*, which is not denuded of fruit till well into January, while the Rowan tree is bare of fruit before October.

The importance of mass or very conspicuous colouring in dispersal is shown by the fact that when only a few small fruits are left on the tree, or the crop is very small, the birds neglect them altogether, and fruits concealed by foliage are not found and eaten.

The greater number of the red-fruited plants in the northern regions ripen their fruit between the end of August and the end of October, but only remain on the trees through the winter. There are a few which ripen their fruits earlier in the summer, like the strawberries and *Aucuba japonica*, and currants, cherries, etc. Most of these are juicy fruits, and supply liquid nourishment, as well as food, in the hot weather, and are also suitable food for nestlings. I notice that a number of brilliant-coloured fruits in England are entirely neglected by birds, even if the weather is very cold and the snow lies deep on the ground. The acid fruits of *Berberis vulgaris* and *Hippophae rhamnoides*, and the pithy ones of *Cotoneaster rotundifolia*, *Pyracantha crenulata*, and some other species, as well as the large fruits of *Aucuba*, seem to be entirely neglected. I have seen the blackbirds eating the common Barberry fruit, but usually all, or almost all, of these are wasted in England, and its wide dispersal by birds and cattle in America is described on p. 365. Many of the north temperate birds, such as blackbirds and thrushes, depend for their food on worms, snails, or insects during the spring and summer, and do not search for fruits; it is only when insects are scarce, and the ground dry or frozen hard or covered with snow, and they cannot get worms, that they turn their attention to fruits, and even in the severe winter blackbirds, thrushes and starlings prefer to

seek for animal food under the bushes or trees, where the ground is soft, than to feed exclusively on the berries waiting for them.

In seasons where there is an excess of berries, naturally a considerable number are wasted, or, rather, are not disseminated by birds, though their seeds may be later dispersed by rain-wash, and this is especially the case in mild winters, when the berry-food is neglected. However, some are eaten every year, and the seeds evacuated germinate, and it is from these that the species is dispersed over a large area.

I noticed, in Kew Gardens, bushes of the American Winter-berry (*Ilex verticillata*), when the leaves had almost entirely, or in some cases quite, fallen, in the middle of November, which were covered with a very showy mass of small red berries, but by December 2nd, all were gone, only the red skins remaining, and not all of these. The red berries are very sweet and juicy, and were clearly more popular than those of the adjacent *Ilex aquifolium*, which were hardly touched at that time. The birds which visited the Winter-berry—bullfinch, hawfinch, blackbird and thrush—in many cases bit the fruit open and swallowed only the pulp and seeds, which latter I found hard by in the excreta. I think the bird which took the interior only, and did not swallow the skin, was the blackbird, which does the same with the white Snowberries (*Symphoricarpus racemosus*). The smaller birds appeared to swallow the fruit whole very greedily. The sweet juicy berries are clearly much more popular than the pithy ones, but acid berries, like those of *Berberis* and *Hippophae*, are left long on the bushes, and often not eaten at all. Pithy berries, like those of *Pyracantha coccinea*, are eaten greedily by blackbirds in the autumn, but a large number are often left, and not eaten till much later, in spite of the winter being severe and animal food difficult to procure. Indeed, in most cases in which the birds feed greedily on berries they seldom completely clear the tree, and when, as in hawthorn or even *Ilex verticillata*, a few are left, these seem not to be eaten, probably because they are not conspicuous enough to attract attention. Even in the case of Rowan trees I noticed that bunches of berries partly concealed by the leaves were not taken, but were left till quite late; and bunches of *Pyracantha* berries, not conspicuous from most points of view, on my bush were, on December 30th, still persisting, though otherwise the tree had been cleared some 2 months or more before. Massed colour is therefore very important for bird-dispersal in temperate regions.

In tropical forests we seldom see coloured fruit in mass. The fruits do not, as a rule, ripen altogether, but irregularly throughout the year, and the birds have to fly far and look out carefully to find them. In such a plant as *Ficus alba*, a low shrub with yellow figs turning red when ripe, you will find one or two red figs on the plant each day, or every few days. The bird eats these, but not the yellow ones. In Black Pepper (*Piper nigrum*), the spikes, when considered ripe enough to gather for trade purposes, bear 1, 2, or 3 red drupes, the rest being deep green. In *Rhodomyrtus tomentosa*, the Rose-Myrtle, the fruits become of a not very conspicuous purple when ripe. In Southern India, where there is a dry season, these fruits apparently ripen largely together, so that the natives can collect enough of them to make jam. In the Malay Peninsula, however, on any day one can only get two or three ripe on a bush, and collecting a sufficient number to make a preserve would occupy a very long time. Each bush bears flowers, unripe and ripe fruit, at the same time. The doves which feed on them, however, contrive to secure every fruit as soon as it is ripe, and, flying from bush to bush, manage to feed well. Though this irregular ripening is the common state of affairs in equatorial regions where there are no seasons, it does not apply to all trees and shrubs, certain trees, e.g., *Ficus benjamina* and *F. retusa*, have definite periods of ripening their fruits (*see* p. 415).

Red-fruited plants, and those in which red forms the attraction to birds,

are mostly shrubs and small to medium-sized trees (rarely large trees), or low shrubby plants or herbs. The chief herbs with red or partly red fruits are *Fragaria* (*Rosaceae*), *Geophila*, and *Nertera* (*Rubiaceae*), *Capsicum*, *Lycopersicum* and some *Solanums* (*Solanaceae*), *Arum* and other *Araceae*, *Neuwiedia Curtisii* (*Apostasiaceae*), while *Scleria sumatrana* with a cylindrical red disc below the achene, and *Carex baccans* with red fleshy utricles, are the only *Cyperaceae* which are attractive by colour to birds.

In the Strawberries (*Fragaria*) the red fruit is composed of a large number of small pulpy red, usually sweet, 1-seeded carpels forming a head. There are a number of species, almost all very similar, spread naturally all over the temperate parts of the world, and sometimes also carried about by man. *F. vesca*, the woodland strawberry, occurs all over the north temperate regions from Iceland to Afghanistan and Tonkin, and from Arctic America to Ecuador. It occurs in the Azores, also in Jamaica apparently wild, and in Bourbon and the Cape, and St. Helena, doubtless introduced. *F. chiloensis* ranges from North-West America and the West Indies to Chile, and to the islands of Juan Fernandez and Hawaii. *F. indica*, a creeping plant with yellow flowers and tasteless but showy fruits, is spread over India, Tonkin, Java and the Philippines. These fruits are certainly distributed by birds, and *F. chiloensis*, which has even reached Hawaii, is said to be dispersed in South America by the wild goose, a class of birds which has a long flight.

Nertera depressa (*Rubiaceae*), a little creeping plant which forms mats or clumps, 3 or 4 inches across, thickly studded in fruit with small but showy orange or scarlet globose berries, each containing 2 seeds, is sufficiently brilliant to be grown as an ornament in our greenhouses. It grows on damp open spaces and banks of streams, and is found in New Zealand, Tasmania, Australia, Philippines, Borneo, Java, the Malay Peninsula, Sumatra and China, in Tristan d'Acunha, Inaccessible Island, to Mexico and in Masafuera and Hawaii. Except in the cold regions of the Antarctic area and the Atlantic islands, it is always a mountain plant, and rather sporadic, at a height of from 5,000 to 7,000 feet.

The very wide distribution of this little plant is due to the attraction of its berries for birds, and Moseley writes (in "Notes of a Naturalist," p. 122):— "The Thrush (*Nesocichla eremita*) of Tristan d'Acunha (an endemic bird) "feeds on the berries of the little *Nertera*." Which birds carry it along the Asiatic and American mountain regions I do not know, but it must be a mountain bird in all cases.

Geophila humifusa and *G. reniformis* are low creeping Rubiaceous herbs which frequent open banks in the Indian, Chinese, Malay and Polynesian regions. The first-named species is very rare, having only been found once in the Malay Peninsula. The second, *G. reniformis*, is far the most widely diffused and most common of any species of the genus. It occurs all over the Asiatic region and into Polynesia, and, widespread as it is, is but slightly variable. The stems creep along banks and throw up erect stems, 1 or 2 inches tall, each bearing a small cluster of white flowers and berries resembling a red currant.

The remaining species, as far as is known, have black fruit, like black currants, and inhabit thicker and denser parts of the forest. Most of them are quite local and comparatively scarce.

Cornus suecica Linn. and *Cornus canadensis* (*Cornaceae*).—These dwarf Arctic Cornels, growing in damp, open moorland in the north temperate zone, have also red fruits, but it can hardly be doubted that they are reduced forms of the shrubby Cornel bushes, which commonly possess red drupes, and have retained the characteristic fruit-colouring.

The Aroids, *Arum maculatum* and *A. italicum*, as well as the tuberous

Amorphophalli, *Arisaema* and *Alocasias* and *Aglaonema*, have conspicuous red berries borne on elongated peduncles, the foliage having quite disappeared before the fruit is ripe. I have every reason to believe that all are bird-dispersed.

Convallaria majalis (*Liliaceae*), the Lily of the Valley, and *Asparagus officinalis*, are also herbs with berries. I have no record of dispersal of the former, but I have found seedlings of the cultivated *Asparagus* springing up in beds in my garden, at a considerable distance from the parent plant, and probably conveyed by birds. The greater number of the species of *Asparagus* are natives of Africa, and are scandent or subscandent shrubs. They all have scarlet berries.

Lycopersicum esculentum, the Tomato.—The wild form of this is a short herb with globose, orange-red berries as big as a cherry, whence it is known as the Cherry Tomato. This form was very abundant among fallen rocks in Fernando de Noronha, and evidently dispersed by birds, probably the local dove, *Zenaida*. It was stated in the island that the large-fruited cultivated forms speedily reverted to the Cherry Tomato. It does not seem to have established itself anywhere else in this way, though it often appears in waste grounds where tomatoes have been thrown away. There are several species in South America, and 2 small-fruited ones, endemic, occur on the Galapagos Islands, undoubtedly evolutions from some small-fruited species brought by birds.

Several of the herbaceous *Solanums* have brilliant red fruits, which are bird-distributed. *Solanum dulcamara* is bird-dispersed. *Solanum biflorum* was not rare in Christmas Island, and is found in Java and the Malay Peninsula in forests; *S. botryophorum* of Fernando de Noronha is a somewhat woody climber with scarlet berries, and there are red-berried forms of *S. nigrum*, which, however, are not so widely distributed as the black-berried form.

Capsicum minimum, the Bird's-eye Chilli, is very popular with birds in spite of—and perhaps on account of—its pungency. The plant is a native of South America, a half-shrubby herb about 2 feet tall, having bright red conic berries, $\frac{1}{2}$ to $\frac{4}{5}$ of an inch long, with many flat fawn-coloured seeds. It is commonly cultivated all over the East, and the dried or fresh fruit is carried about by Malays, Indians and others, as a condiment. Though it occurs more or less established around villages, it has not spread or been dispersed by birds, so far as I have seen, except in a few instances. It is to be found in great abundance on the limestone precipices of the Batu caves in Selangor, in quite inaccessible spots near the mouth of the caves, where Malays and Indians frequently hold picnics, and perform religious ceremonies. The fruits were doubtless brought for food, and, some being thrown away there, the birds, probably the Limestone Blackbird (*Myiophoneus*) which is common there, had eaten the fruit and deposited the seed in its excreta high up on the precipices, where it grew far out of the reach of natives. In Fernando de Noronha I found it widely scattered in the bushy parts of the island, the seed having been disseminated by the doves, *Zenaida maculata*. I have not seen the larger-fruited kinds, *C. annuum*, etc., so dispersed, but C. Boden Kloss (in "Andamans and Nicobars," p. 3) writes :—"Numbers of Blyth's doves (*Macropygia rufipennis*) "frequented the scrub near the village (on Kachal Island, Nicobars). We "were astonished to find the crops of all those shot completely filled with "large red chillies."

The Capsicums were introduced to the East Indies in 1540, and spread in cultivation everywhere, and it seems curious that the plants have established themselves so little, as wild plants, about the world. They do not appear to occur in oceanic islands until brought by man. *C. minimum* seems to establish itself only in dry rocky spots.

Neuwiedia Curtisii (*Apostasiaceae*).—All the species of *Neuwiedia*, with the exception of *N. Curtisii*, possess 3-angled green capsular fruits, which dehisce and discharge a large number of very light seeds which are dispersed by wind, but this exceptional species has nearly round red berries containing a large quantity of minute, round, black seeds. It is a native of Penang and Singapore, and so very closely resembles in flower the capsuliferous *N. Lindleyi* that it can only be readily distinguished by its broader leaves, and Wallich, finding it only when in fruit, mistook it for a Liliaceous plant.

Parallels to this transformation of a capsule into a berry may be seen in *Xiphidium floribundum*, of Mexico, in which the fruit appears to be developing as a capsule, but, on ripening, the pericarp swells so as to fill the cells, and the whole fruit becomes orange-coloured; and in *Dianella*, in which the whole fruit becomes pulpy and blue or white, as mentioned in the section dealing with the transformation of capsules to berries (*see* p. 422).

Trees, climbers and shrubs with the red drupes or berries attractive to birds, are very abundant all over the world, and are to be found in many orders. A list of them would be too extensive to give. It is noticeable that red drupes and berries are almost always small, 2 mm. to as much as ½ inch through; easily swallowed by a bird as big as a starling or thrush.

In *Eugenia*, for instance, the red-fruited species like *E. microcalyx* have fruits not bigger than a Holly berry; the big ones, *Jambosa* section, have white or plain green fruits (occasionally, but very rarely, pinkish), destined for dispersal by bats, monkeys, and civets. When large fruits are to be dispersed by birds, and red colouring is necessary to attract, the fruit is usually provided with a red aril, or the capsule is red, the eatable seeds black or orange, or the rachis is coloured red, to call the attention of the birds. The biggest red berries for bird-dispersal I know of are the fruits of *Trichosanthes* and some other *Cucurbitaceae*. In these the fruit is torn to pieces by crows or such birds, and the black or orange pulp containing the seeds swallowed.

That the kind of bird catered for affects the colouring of the fruits is shown by the genus *Empetrum*. Where grouse, which fly low and short distances over the moorlands, are abundant, as in the north temperate zone, the fruits are black. These birds, absent in the southern regions, are replaced by Thrushes (*Turdidae*), and such birds which fly high and long distances, and the fruit is red.

I give here some account of the more interesting red-fruited trees or shrubs in their relation to birds.

Ilex.—The hollies are a very widely distributed group of trees or shrubs, occurring all over temperate and tropical regions, but most abundant in the tropics. The whole order is dispersed by birds, the fruit being 2- to 4-seeded berries, red, black, or pink in colour and small, not juicy but firm-fleshed. They are borne usually in short cymes, rarely in racemes. The seeds are usually flat on one side and rounded on the other, and rather large in proportion to the fruit. The trees are generally evergreen, but the Winter-berry of America sheds all its leaves in winter, so that the bright red fruits are conspicuous and quickly cleared off by birds. I have already given an account of this plant on p. 394. The temperate region trees all fruit at the same time in the winter. In tropical trees, such as *Ilex cymosa* and *I. macrophylla*, the fruits ripen quite irregularly, 1 or 2 being ripe at a time on a cyme. They are therefore not very conspicuous, but are sought for by bulbuls and other rambling fruit-eaters. The berries of the common English holly are apparently not eaten by birds till the winter has well set in, and food is scarce, when they are sought after by blackbirds, thrushes, and such small birds, and even by pigeons in hard times. This plant, which appears in England as early as the Pliocene era, occurs all over Europe as far north as Southern Norway. The genus is absent apparently from temperate Asia, except Sachalin, China, and Japan, but is well represented in

tropical Asia and Africa, and America from Newfoundland to Paraguay. Two species occur in the Canaries, Madeira and the Azores, which is the only oceanic island group in which the *Ilex* seems to occur.

The wide distribution of the genus and its abundance are due to its conspicuously coloured berries being very attractive to birds.

Rhus (*Anacardiaceae*).—The fruits of the Poison Oaks and Poison Ivies seem to be extraordinarily popular with birds. Many of these plants are poisonous, and the small drupes, though borne often in large bunches, are apparently neither very brightly coloured nor conspicuous. In R. *coriaria*, of South Europe, the drupes are bright red, and in R. *glabrum* and some of the other species more or less tinted with the same colour. Those of R. *toxicodendron*, very popular with birds in America, are greyish-white in colour. The genus has a very wide distribution, species being found in Southern Europe, the whole of Africa and Arabia, Madeira, the Canaries and Azores, Madagascar and the Comoro Isles, India, China, the Malay Peninsula (1 species only and that rare); Borneo, Java, Celebes, Ternate, Philippines, New Guinea, Australia, many Polynesian islands, and the whole of America from the north to Chile. They are absent from New Zealand, Ceylon, Christmas Island, Cocos-Keeling, Krakatau and Fernando de Noronha. The genus, in fact, appears to be absent from very cold climates, and is comparatively scarce in the tropical rain-forest region. Leaves of plants believed to belong to the genus are found in the Cretaceous and Miocene rocks of the north temperate zone.

In North America, where they are very abundant, they are very popular with birds, as a list received by me from Mr. Henderson contains no less than 51 kinds of birds which feed on them.

The allied genus *Buchanania*, of the Malay regions, has similar small drupes, reddish in colour, and is widely distributed and common over the Indo-Malayan region.

Pyrus aucuparia, the Rowan tree, belongs to the section *Sorbus* of the genus *Pyrus*, which contains two series of trees, *P. aria* and its allies, with small inconspicuous fruits like wild pears, green or yellow in small corymbs; and the *P. aucuparia* section, with pinnate leaves and large showy corymbs of juicy scarlet fruits. All the pears (*Pyrus*) afford food for birds, but far the most popular are the brilliant fruits of the Rowan tree. I have a list of 14 birds which feed on them. The list would doubtless be larger but for the fact that the birds which eat them, especially those of the thrush family, attack the fruit so speedily, as soon as it is ripe, that a couple of blackbirds will clear a tree covered with fruit in 2 days, and other birds do not get a chance at them. They are the first fruits devoured by the birds in the autumn.

The Rowan tree grows as far north as Labrador, and in most of Europe and Northern America, for the American species is hardly distinguishable from it, as Asa Gray admits. The tree is a native of the mountains of the north, though often cultivated in the south, but has failed in most cases to establish itself away from the colder northern mountains. It is, however, readily diffused over the British Isles by the birds, and is the most abundant of the genus in our woods, thanks to its brilliant sweet juicy berries.

YELLOW FRUITS.

Yellow is not so common a colour as red in drupes and berries, nor is it so conspicuous, though it is frequent in capsules and in arils. It has also a tendency to pass towards orange and so to red.

Among the more conspicuous yellow berries are those of the American *Duranta* (*Verbenaceae*) and the small pulpy ones of *Urophyllum* (*Rubiaceae*), Malayan shrubs in dense forest, with short axillary cymes of a few orange-

yellow berries. *Canthium horridum* (*Rubiaceae*) is a spiny shrub in open country in Indo-Malaya, with a globose acid yellow fruit as big as a cherry, and *Gmelina asiatica* and other species (*Verbenaceae*), also open-country plants, have berries so similar to those of the *Canthium* that the Malays call them by the same name. *Strychnos pubescens* (*Loganiaceae*), a climber, which seldom flowers or fruits, has also a similar fruit, globose, ¾ inch through, but intensely bitter, containing brucine, and is eaten by birds, though the whole plant is poisonous.

Chrysophyllum Roxburghii (*Sapotaceae*), a Malayan tree, has pulpy yellow fruit 1½ inches through, contrasting with the deep green foliage, it is sweet and eaten by birds. A number of the shrubby figs and some fairly big trees have orange-yellow figs. *Pyrus floribunda*, of Japan, has small yellow pears, fairly conspicuous among the foliage, but still more so when the leaves have fallen, and I observed that they were more popular in Kew Gardens with the birds, especially starling, jay, and blackbird, than the bright red fruits of *P. baccata*, the Siberian Crab, being eaten first.

The drupes of the widely-distributed genus *Celtis* (*Urticaceae*) are often yellow, though some of them possess black fruits. The Hackberries range all over the world, South Europe, Northern Africa and Madeira and tropical Africa, temperate Asia to China and Japan, India, Ceylon, Andamans, Siam, to the north of the Malay Peninsula at Perlis, Java, Christmas Island, Philippines, Polynesia, Mascarene Islands, all over America and the West Indies.

The drupes vary from the size of a small pea to that of a cherry, and have a black, purple or yellow sweet pulp surrounding the stone. Of *C. occidentalis*, of North America, the trees so labelled at Kew have very small orange fruits, which I have seen being greedily devoured by song- and missel-thrushes and blackbirds. Sargent, however, describes the fruit as dark purple, and from ⅓ to ⅔ inch through. They are much sought after in America by birds. The Christmas Island species, *C. cinnamomea*, is a native also of Java, India and Ceylon. The fruits I saw were pale green, as they are shown in Trimen's "Flora," but they are probably yellow when ripe. The Christmas Island pigeon appeared to be feeding on them and the flowers.

The allied genus *Gironniera*, of which a few species are distributed over the forests of India, China, and the Malay Peninsula and islands, have similar small orange-yellow drupes, which are eaten by pigeons. They are all trees about 40 feet tall.

A considerable number of the genus *Schefflera* (*Araliaceae*), mostly epiphytic shrubs or small trees of tropical Asia and Polynesia, have yellow fruits of small size, undoubtedly disseminated by birds. One species, of which the fruit is unknown, but which is very closely allied to a yellow-berried one, is found in Christmas Island.

On the whole, the orange- and yellow-fruited plants are most characteristic of open woods and rather thin jungle, or open plains.

Pink Fruits.

Pink-coloured fruits are by no means common, and, as a rule, are not very conspicuous. *Euthemis leucocarpa* (*Ochnaceae*) and *Pernettya angustifolia* have white, rose-pink, and red berries. *Cissus Hookeriana*, a tall slender Malayan vine in thick forests, has pink translucent grapes as big as a large cherry; as they hang down in the forests from high trees, they are very showy. *Lettsomia*, a genus of *Convolvulaceae* in tropical Asia, has rather showy pink berries, and the fruits of *Sabia limoniacea* (*Sabiaceae*), a climber in Malay forests, and the seeds of some of the scandent *Gnetums*, are also rose-pink. The small fruits of the low shrubby *Ilex Griffithii*, of the tropical Asiatic mountains, are pink, and closely resemble those of the *Vacciniums* which grow

with it. The berries of the Rose-myrtle (*Rhodomyrtus tomentosa*), a bush, abundant in open country in India and Malaya, are also pink, with a purplish tinge when quite ripe; the Doves (*Turtur*) usually eat them as fast as they ripen. In many species of *Glochidion* (*Euphorbiaceae*) the brown capsule dehisces and falls off, leaving exposed the seeds with a thin pink coat; these are much eaten by birds.

Brown-Purple Fruits.

This is not a common colour in fruits. It is conspicuous in *Pratia begoniaefolia* (*Lobeliaceae*) and *Crawfurdia Blumii* (*Gentianaceae*) a slender climber in grassy spots, and it is also noticeable in *Flacourtia Rukam*, a low tree. The colour is usually intermediate between black and red. In the herbaceous plants *Pratia* and *Crawfurdia* it is quite showy against the foliage surrounding them. There are a good many fruits with blue-purple colouring, *Eugenia*, *Vaccinium*, *Vitis*, etc., sufficiently conspicuous to attract birds.

Black Berries and Drupes.

Black is the second most common colour of fruits. It is chiefly found in the fruits of shrubs, trees and climbers, occasionally in herbs, and these are plants of more or less open country. In most cases these black fruits are smooth and polished, the light reflected from them making the fruit more conspicuous. In some there is a bluish bloom (*Mahonia*), which produces a blue or pale whitish tint, contrasting with the green foliage. In some cases, too, the peduncle, rachis, bracts, sepals or disc, are coloured red or white, to set off the black fruit and attract the attention of passing birds to it.

In some of the bigger trees the black fruit is rather large, and comparatively inconspicuous; such trees as *Dialium* (*Leguminosae*), *Parinarium Griffithianum* (*Rosaceae*), *Cinnamomum*, and, indeed, most of the *Laurineae*, nearly all of which have black fruit, which are not too big for fruit-bats and the larger birds. These large black drupes are closely associated with pigeons, especially *Carpophaga*, and in temperate regions *Columba*, which feed largely on Laurineous fruits, while *Dialium* and such fruits are the food of fruit-bats, civets and monkeys.

The greater number of black fruits, however, are small drupes or berries, by no means too small for birds of the size of blackbirds or bulbuls.

The only black-fruited low herbs I have met with are some species of the genus *Geophila* (*Rubiaceae*), *G. melanocarpa*, and *G. pilosa*. These are natives of the dense forests of the Malay Peninsula. In the former species the shining black berries are borne on the top of erect stems, 3 inches tall, and quite conspicuous; in the latter the stems are hardly as tall. It is interesting to note that these black-fruited *Geophilas* are very local, and by no means as widely distributed as the red-fruited *G. reniformis*, which occurs all over the Indo-Malayan, Chinese and Polynesian area. Black fruits, as a rule, are little represented in the dense forests, though they occasionally occur there, but, when they do, they usually have red or yellow rachis, or corymb-branches, to set them off. The greater number are found on open country plants where the birds can easily detect them.

Tall Herbs.—There are some fairly tall herbs, from 2 to 3 feet high or even higher, which have black fruit and which are worth notice.

Clidemia hirta (*Melastomaceae*) is a nettle-leaved hairy herb, 3 feet tall, with small white flowers and black berries like very small currants, borne in small clusters in the leaf axils. It is a native of South America, and has somehow contrived to establish itself in Java and in Fiji Island, and the Malay Peninsula.

A very dull, uninteresting, and useless plant, it is difficult to see how it ever got to these places. The fruits are, however, very popular with birds. In the Malay Peninsula it was a common weed in the Botanic Gardens, where it was distributed in shady spots. I also found abundance of it in one wood near the Reservoir, about 4 miles away, and it was common in Seremban (Negri Sembilan), very many miles away. It is just possible that it got to these spots in pot plants sent out from the Botanic Gardens, but, though usually growing in great abundance where it occurred, it did not spread from these centres, as might be expected, between these localities.

Wulfia stenoglossa (*Compositae*), a yellow-flowered Composite, with the almost unique peculiarity in the order, of the achenes becoming juicy and black, forming a head resembling a blackberry, was introduced into the Botanic Gardens, Singapore, where it was used as a bedding plant. It is native of South America. Soon after it fruited it was dispersed by birds—probably the Bulbul (*Otocompsa analis*)—and appeared in abundance about 100 yards away, and persisted as a weed for some 14 years after its cultivation had been given up. It did not spread outside the Gardens, so far as has been recorded. The reason of this limited area, in spite of the abundance of plants in *Clidemia* and *Wulfia*, appears to be that the small birds which eat the fruits and distribute the seeds do not fly to any great distance from the source of their food supply, as long as there is sufficient food to maintain them. They settle down into a garden or thicket, and nest there, and their progeny, finding no reason to leave, continue to remain in the same locality. The Singapore Gardens abound in birds of this type, and though these birds fed and distributed the seeds of many plants, they never went more than a few yards outside the Gardens, so that the seeds which they swallowed were evacuated in, or just outside, the Gardens, where the birds habitually lived. It is for this reason largely that such plants introduced into gardens or cultivated areas do not spread as extensively as would naturally be expected. Where berries and drupes are comparatively scanty, the birds have to fly over wide tracts of the country in search of food, and scatter the seed as they go, but where food is abundant they make their homes permanent.

I will add here some notes on two other plants which illustrate this point. Though they are not herbaceous plants, they are both dwarf, and are dispersed by similar small birds.

Brucea sumatrana (*Simarubeae*) is a low shrub about 5 feet tall, with very small, intensely bitter drupes. It is usually to be found in open heathy country, and is abundant in such localities in the Malay Peninsula. It was found by Dr. Wallich in Singapore, in 1822, but later had almost completely disappeared. I did, however, find a few plants still persisting in the old Chinese cemetery near the town. As it was required for investigation as a drug, I procured seeds from the east coast of the Peninsula, and planted a considerable quantity in the Botanic Gardens. In a few years, aided by the birds, it had spread along the hedges about a ¼ mile away in abundance, but only in the vicinity of the Gardens.

Wikstroemia Ridleyi (*Thymeleaceae*) was a low slender shrub with few red drupes of small size. I brought this rare plant from the sand-hills of the Pahang River and planted it in the Gardens, where, after a few years, it disappeared. Several years later, however, specimens were sent to me as a new plant from the hedges and waste ground about ¼ mile away, where it had been clearly planted by birds.

In both of these cases the plants were inhabitants of open and more or less sandy localities, which class of country was not to be found in the district, though both grew well in ordinary garden soil, and no doubt the competition of stronger-growing weeds had an influence in restricting their spread. Still,

the fact must be noted that seeds were not carried to more distant parts of the Garden, or elsewhere than these localities close to the original plants.

Returning to herbaceous plants with black fruits, we next have the Pokeweeds of America and temperate Asia, *Phytolacca* (*Phytolaccaceae*), coarse and often large perennial herbs with dense spikes of numerous black shining berries. Kerner mentions that when he fed *Phytolacca* berries to a song-thrush, it sickened; but in my garden the blackbirds eat greedily the fruits of *Ph. clavigera*, generally regurgitating the seeds, and in the open woods of Berastagi, Sumatra, 5,000 feet altitude, I found *Ph. decandra* scattered about at some distance from any garden in which it could have been planted, and undoubtedly dispersed by birds. Kalmbach mentions the seeds of this plant as having been found in the crop of the American Crow (*Corvus brachyrhynchos*). It spreads widely from gardens wherever it has been introduced, even in the Mediterranean region from Portugal to Greece. *Ph. octandra*, which has been introduced into New Zealand, according to G. M. Thompson, is widely spreading, and is eaten largely by pheasants, and causes their flesh to become dark (l.c., p. 471).

Solanum nigrum L. (*Solanaceae*).—This weedy herb is very common in waste ground in England, and it, or forms of it, occur in similar places nearly all over the world. The small berries are black, but not conspicuous in the common form, being rather hidden below the leaves. It often happens that the fruit, although ripe, remains green. While I have seldom, if ever, seen black berries on the plant in my garden, it constantly appears as a weed in the beds and in flower-pots, and from its constant growth along the road and street sides I have little doubt that it is largely dispersed by rain-wash. It does not appear to be a native of England, and has not been found in a fossil state. I have never seen it in any place where it looked indigenous, and Gerard calls it the Garden Nightshade, saying that it grows in gardens and by highways, etc. (1597). Various forms of what seems to be specifically the same plant are known under the name of *S. oleracea* all over the tropics, and used as a vegetable by natives, but I have never seen or heard of it being cultivated anywhere. The red-berried form, already alluded to (p. 396), is less abundant than the black-berried forms. I have no doubt that this plant is mainly bird-dispersed, though in cultivated areas it certainly spreads more by rain-wash.

A small number of the baccate *Liliaceae* have black fruits, though in most the fruits are red. Such are *Paris quadrifolia*, a herb of European and North Asiatic forests, the North American *Trilliums*, some species of *Polygonatum*, and the *Disporums* of temperate and subtropical Asia. All these plants haunt rather open forests and woods. The berries are probably eaten by ground-game, pheasants, etc. *Alpinia melanocarpa* (*Zingiberaceae*) also has black berries (though most of these *Alpinias* have red or orange fruit), it inhabits damp open country, and is about 4 feet tall.

Trees with black fruits or berries are usually small, from 20 to 30 feet tall, with the main exception of the *Laurineae*, and the fruits are quite small. Such are *Rhodamnia trinervia* (*Myrtaceae*), a low bushy tree, or a shrub at high altitudes, with very small black berries, hardly $\frac{1}{8}$ inch through, common in the Malay Peninsula, and extending from Tavoy and Siam, through the Malay Islands to Australia. The fruits are very popular with pigeons and bulbuls. The tree inhabits open country and woods. The lower bushy allied plants, *Nelitris*, *Myrtus* and several other Myrtles, have similar berries, and grow in similar spots. The *Laurineae* vary in height from about 12 feet to 100 feet or more. In nearly all the fruit is a black, sometimes blue-black, drupe with very little pulp. In a few genera the peduncle (*Dehaasia*), the cup formed by the accrescent perianth (*Cinnamomum* spp., *Litsea* sp.), or the panicle-branches (*Phoebe*), enlarge in fruit and become red, and in some species of *Litsea* the

ripe fruit is pink, or yellowish, or red, and more pulpy. The black-fruited kinds seem, in spite of their scanty pulp, to be popular with pigeons. *Cryptocarya nativitatis*, of Christmas Island, was one of the most favourite fruits with the large *Carpophaga* of the island.

Bushes with Black Drupes or Berries.—Among these we have such plants as the Privets (*Ligustrum*), and *Olea maritima* (*Oleaceae*), *Premna* (*Verbenaceae*), *Rhamnus catharticus* (*Rhamnaceae*) the buckthorn, several species of *Cornus*, *Sambucus nigra*, *Ardisia littoralis* (*Myrsineae*), all of which are open-country plants, and are much sought after by small birds. The fruits are all small, and suited for birds the size of bulbuls or greenfinches. Larger birds do not seem to be attracted by the very small fruits. I observed Greenfinches (*Coccothraustes chloris*), in Kew Gardens, greedily devouring the minute fruits of a *Cotoneaster* (*C. bacillaris*). These fruits were a kind of fuscous green, nearly black, but not at all conspicuous. The blackbirds, which were abundant all round, preferred the larger sweet black fruit of *C. Wallichii*, a small bushy tree of the Himalayas. Large-sized birds, such as fruit-pigeons and hornbills, do not seem to care for tiny fruits on small bushes, but look out for something bigger, and on higher trees.

Hypericum androsaemum (*Hypericineae*) possesses some interest. It is a low, shrubby plant which produces globose, black, flavourless pulpy fruit. This is unlike almost any other species of the genus, which have dehiscent capsular fruit. The seeds are very minute. The fruit ripens in September, but after a month or so, if not eaten by birds, it dries up, and thus remains quite uneatable through the winter, when it falls off, breaks up, and the seeds are dispersed by wind and rain. I have watched a bed full of this plant in Kew Gardens, covered with fruit in the baccate stage for several years, and have never seen any bird eating the fruit, nor any signs of its having been touched by them, though the fruits are a very conspicuous shining black. The plant was introduced into New Zealand, and G. M. Thompson (in " Naturalisation of Animals and Plants in New Zealand ") states that birds eat the fruit, and so spread it about in the islands. E. Atkinson says that the fruit in New Zealand is quite fleshy and berry-like, and decidedly attractive to birds.

This is an example of the method by which a capsular fruit can be converted into a baccate one by merely a local change of environment. Dehiscence of the capsule is delayed long after the seed is in a state for germination, and, strictly speaking, in this plant no dehiscence takes place at all, except that frequently the dried fruit opens a little at the top, so that the seeds may fall out; but often even this does not occur, and the capsule falls off with an irregular opening at the base, through which the seeds escape. It would be easy to understand that, in cases where bird-food was scarce, the fruit of this plant would become entirely baccate, as has happened in the blue fruit of *Dianella* and the orange fruit of *Xiphidium*. In *Hypericum hircinum* and *H. elatum* the conical fruit is fleshy at first and reddish in colour, quite conspicuous. I cannot find any evidence that birds eat these fruits, but it is noteworthy that *H. elatum*, an introduced plant grown in shrubberies, has appeared in several parts of England and Scotland, at some distance from gardens.

Melastoma malabathricum and *M. polyanthum* are bushy shrubs occurring in great abundance in open country in India and Malaya. They are usually from 3 to 8 feet tall. The fruit is a berry of a dull pinkish colour, covered with hairs, and quite inconspicuous. When ripe, the fruit dehisces transversely, usually about halfway across, and quite irregularly, and exposes a conspicuously black jam-like mass full of very small seeds. This is most attractive to birds, chiefly bulbuls and turtle-doves, who eat the sweet jam-like pulp and swallow it with the minute whitish seeds, and the plant comes up everywhere in open country, or in fields of the troublesome grass Lalang (*Imperata cylindrica*). So

freely does it come up that it frequently evicts the Lalang, and prepares the way for reafforesting such land.

In Perlis, in the northern part of the Malay Peninsula, I found another *Melastoma* on an open heath in which the fruit dehisced, or split on one side vertically, the walls of the pericarp reflexing and spreading so as to expose the pulpy black mass (*M. schizocarpa*). There are a number of species occurring in the denser forest, but I have never seen the fruits of any of these dehisce so as to expose the pulp, which I do not think is black. It is interesting to note that *M. polyanthum* was established in Krakatau in 1906, 23 years after the destruction of the vegetation by the eruption.

Heath Shrubs (*Vacciniaceae* and *Empetraceae*).—All the moorland districts, both lowland and montane, of the north temperate regions of Europe, Asia and America, are covered to a large extent with low bushy evergreen shrubs, of which a number possess small sweet globose berries, usually black, but sometimes with a bluish-bloom on them which serves to contrast them with the dark green foliage. These plants belong to the orders *Vacciniaceae* and *Empetraceae*. Some of these baccate heath plants, however, have red fruits. Thus, while *Vaccinium myrtillus*, *V. uliginosa*, *Andromeda polifolia*, *Arctostaphylos alpina* and *Empetrum nigrum* have black berries, in *Vaccinium Vitis-idæa*, *V. oxycoccus*, *Arctostaphylos uva-ursi*, *Empetrum rubrum* and *E. Eamesii*, the berries are red. Of these, in the northern area the most abundant and widely-spread plants are those with black or blue-black berries. On these moorlands frugivorous small birds are scarce, the chief one in Europe being the ring-ousel, but they are haunted by numerous grouse and ptarmigan, which feed on the shoots and berries of the *Vacciniums* and *Empetrum*. These birds (*Tetraonidae*), though they can fly well for long distances, do not search for food by flying high and quickly over the ground from one spot to another, as the thrushes and small fruit-eaters do, but settle down in one spot, and walk about eating the berries and shoots of Bilberries and Crakeberries which they find there. Bright colours, therefore, as an attraction from a distance, have no value for these birds, though they are important for thrushes and such birds. We shall see that in the case of *Empetrum*, where grouse are absent, the berries are red, and dispersed by the higher-flying rapid birds.

Vaccinium (*Vacciniaceae*).—This bird-dispersed genus is spread over a very large part of both hemispheres, but is most conspicuous in the north temperate zone, where the mountains and moors are often covered with an immense abundance of low bushes of the various kinds. They are more scarce in the tropics, where, with the rest of the plants of the order, they are mainly confined to the mountain tops, though close to the Equator we find several species (*V. malaccense* and *V. Hasseltii* of Malaya) growing in open places near the sea at sea-level. The plants range in size from low shrubs to fairly large trees in the Malayan region, even in the same species. On the mountains of Java the beautiful *V. waringiaefolium* may be found flowering and fruiting, from a low shrub, under a foot tall, to big stout trees from 40 to 60 feet high.

A few species are epiphytic, as *V. Hasseltii*, an epiphyte in the forest, but a low tree or large shrub on the sand-hills near the sea. The fruits of these Bilberries are small, round, few or many-seeded berries, black or deep blue, often with a glaucous bloom, red or dull pink, and usually conspicuous. I have a list of 33 kinds of birds which feed on them, mostly from the temperate northern area. Those of the tropical regions have not as yet been recorded. In the Arctic and sub-Arctic regions the most important disseminators are the grouse tribe (*Tetraonidae*), aided by many other northern birds, and by the mammals, bear, reindeer, etc. The lists of fruit-food birds and mammals are given under the head of Dispersal by Mammals and Birds, pp. 340, 451. In the tropical mountains the mountain birds, which fly from

range to range, disseminate them readily over extensive areas. The fruits in most of the heath-like shrubs, at least in the northern region, are black or plum-colour, and also those of many tropical species such as *V. malaccense* and *V. Hasseltii*, and have similarly coloured berries. There seems a tendency in allied plants to retain the same fruit-colouring throughout the order.

The *Vacciniums* push into the Arctic region, as far as any plants can go, in both hemispheres, and are abundant in Europe and North America, and in the tropics in South America as far south as Guiana, Peru and Columbia. They are scarce in Africa, only found in the South, and Madagascar, and are absent from the other islands. Fairly plentiful in the whole of Asia, especially in mountains in the south, Java, Sumatra, etc. As island plants they occur in the Azores, Madeira, Canaries, New Hebrides, Sandwich Isles, Samoa, and in New Zealand, but are absent from Australia and distant oceanic islands.

The allied genus *Gaylussacia* takes its place in Brazil, and the fruits of the species which are met with in North America seem to be as popular with birds as are the berries of *Vaccinium* elsewhere.

Vaccinium is one of the genera which is able to live both in the Arctic regions and on the Equator, which—accompanied by its value as a food for birds of all kinds—accounts for its very wide distribution.

Empetrum nigrum (*Empetraceae*).—The Crake-berries are heath-like plants inhabiting cold moorland regions, and are often found with the *Vacciniums*. There are 3 or 4 very closely allied species of *Empetrum*, with black or red berries, *Corema album* of the Azores and Portugal, and *C. Coradinei* of North America, with rather inconspicuous, white or orange, 2-seeded berries, and *Ceratiola ericoides*, with small orange berries, sessile on the branches and very inconspicuous. The last two genera are rather local, the fruits not being at all showy, though *Corema album* has evidently been transported by birds to the Azores from Portugal.

The *Empetrums* are much more interesting. *E. nigrum* has quite conspicuous, black 6- to 8-seeded berries, which are very attractive to birds, and I have a record of 23 species of birds which feed on the fruit and so disseminate the plant. Its distribution is very extensive all through the Arctic and temperate regions, going as far north as any shrub can go. It is found in Scotland, and in England as far south as Poole in Dorsetshire, in the mountain regions of Southern Europe, and the sandy heaths of Belgium and Holland, as far as Montenegro and Laristan, Siberia, Kamschatka, Sachalin, Japan and Arctic America. It is absent from the Himalayas and the African mountains, and from all tropical regions. In Britain the plant first appears in the Interglacial beds of Scotland, and it is interesting to note that, though this very widely-spread plant only appears at that period, the much more local genus *Corema* has been found fossil in the earlier Tegelen beds of the Upper Pliocene.

Though the fruits are eaten by other kinds of birds, its distribution is closely associated with that of the grouse, and it seems to be only absent from districts where these birds are not to be found, or where there is no reason to believe they did not formerly exist.

E. rubrum.—In the Antarctic regions we get this species, which is chiefly distinguished from *E. nigrum* by its having bright red, not black, berries. Sir Joseph Hooker formerly considered these two plants to be forms of one species. The red Crake-berry replaces the black one in the south. It is found in Chile, Patagonia, Hermite Isle, Cape Horn, Falkland Isles, Masafuera and Tristan d'Acunha. In these localities the grouse are absent, and as the fruit-eating birds of Tristan d'Acunha consist only of a thrush, a finch, and a gallinule, it is probably the thrush which is responsible for conveying the seed to this island. However, the Antarctic skua also haunts the spot, and we have on record that the northern skua, a bird allied to it, has been seen feeding

occasionally on the berries of *E. nigrum* in sub-Arctic regions. It is clear that the colouring of the berries of *E. rubrum* is effective in inducing frugivorous birds to eat, and so transport, the seeds. There are, however, two other red-fruited forms or species, *E. Eamesii* and *E. atropurpureum* (Fernald, in Mem. Gray Herb., ii, 309) about the Gulf of St. Lawrence in eastern North America.

Juniperus.—The somewhat inconspicuous, greenish-black berries of Junipers seem to attract birds, and even mammals, all over the north temperate region, where these plants grow. The number of birds in Europe and North America which feed on them is very large, and Prof. Bray states that raccoons, foxes, wild-cats, and chipmunks also consume large quantities of them and pass the seeds in their excreta, and Phillips gives an account of the seeds being brought by cattle from Texas to Kansas. (*See* Domestic Cattle, p. 364.)

The following notes, taken from "Dissemination of Junipers by Birds," by F. J. Phillips (*Forest Quarterly*, viii, no. 1, p. 1), are of some interest :—

Juniperus virginianus grows in Maryland and Kentucky in uncared-for fence-rows, and a long line of Cedars (i.e., *Junipers*), from which the fences have disappeared, often indicates the boundary lines. The frequent appearance of all or of a majority of Juniper trees on one side of a fence is usually due to the birds facing the wind when they evacuate. In the sand dunes bordering Lake Michigan, 60 to 80 per cent. of the growth of *J. virginianus* and *J. communis* had resulted from dissemination by birds. Only one to a few seedlings were found beneath each tree. In New Mexico 90 to 95 per cent. of all the reproduction of *J. monosperma* and *J. pachyphloea* was by birds. A Silver Maple grove at Rockford, Illinois, showed the result of bird-dissemination of *Juniperus virginianus* 186, *Prunus virginianus* 26, *Asparagus officinalis* 25. Robins (*Turdus migratorius*) were seen to feed on Juniper, and then fly to pasture lots and excrete seeds when resting on herbs or shrubs.

The large number of birds which feed on the berries of the Juniper, especially as many of them are wide-wandering birds such as the thrush family, is enough to account for the wide dispersal of the Junipers, of which there are about 25 recorded species, ranging over the whole Arctic region from the Arctic circle in Europe, Asia and North America, as far south as Algeria and the Himalayas, Florida and the West Indies, and to the islands of the Canaries, Madeira and the Azores. The common *Juniperus communis* is stated by Elwes to be more widely distributed than any other tree or shrub in the northern hemisphere. It extends all through Europe from Lapland to the mountains of the Mediterranean countries, all through northern Asia to the Tianshan range (but is absent from Japan, where it is replaced by *J. rigida*), and Asia Minor, Persia and the Himalayas as far as Kumaon, and the whole of North America as far south as New Mexico. According to Reid, it has not been found fossil in Britain, but it occurs in Interglacial beds on the Continent. The berries of Juniper seem to be derived from the more typical cone fruit of the *Cupressineae* group, where the ovule-bearing scales, few in number, are woody, and separate when ripe, letting the seeds fall out. In the Juniper, the scales have become fleshy and connate, and form a berry. Traces of the vanished scales are to be seen on the fruits, and a faint edge on the seed is the last remains of the wing of the wing-seeded *Cupressus*. The Junipers then, may be taken as a later evolution of the *Cupressineae*, but occupy a vastly larger area than any species or genus of the latter group, and owe their very wide distribution and abundance to the transformation of a cone of scales to a soft and eatable berry, beloved of birds. Their persistence in an edible form through the winter in the cold regions, when most other berries have disappeared, adds much to their advantage in dispersal by birds. It is worth noting, too, that the species with the smallest fruit and seed is the most widely distributed, as smaller birds can swallow it.

Sambucus (*Caprifoliaceae*), the Elderberries, is a small genus of few species occurring in temperate regions, Europe, North America, India, Java, Sumatra and Borneo (1 Malayan species), tropical Africa 2, one perhaps introduced; Australia 2, allied to the Malayan one; 1 species in Madeira and another in the Canaries; 1 species has run wild in the West Indies. These bushes have small black or red, rarely yellow berries, very sweet and juicy, and popular with birds, of which 29 species are recorded as eating them. Every observer has noticed how constantly Elder bushes keep coming up in waste ground, old ruins, and such places, from seed sown by birds. The plants mostly grow in open country, rather than in woods, but the Malay one I have seen on the edges of streams in dense forest in Sumatra, at 5,000 feet altitude. They do not appear to be dense shade-loving plants, nor do they like very cold regions or extreme heat, but temperate regions only. The common Elderberry (*Sambucus nigra*) first appears in Interglacial beds in England.

The South African shrub *Osteospermum moniliferum* is interesting as being one of the very few *Compositae* which have fleshy, eatable black fruits, like *Wulfia* already mentioned (p. 401). The achenes are almost black, and are eaten by natives and children. The genus consists of 50 species, all African. This one is the only shrubby one, and apparently the only one with eatable fruit; the rest of the species are herbs.

One of the most-rapidly dispersed plants with black fruit is *Lantana mixta*. This shrub was introduced into Asia from South America, obviously as an ornamental plant for its showy red and yellow or rose-coloured flowers, and very speedily spread all over the open country. It seems to have been introduced into Ceylon about 1824, and rapidly spread over cleared ground and abandoned estates, till in many places it formed impenetrable masses. It spread in like manner all about the open country in Singapore and Malacca, being at one time the most abundant and conspicuous plant. The little black drupes in a head are very attractive to small birds, and it has in this manner spread all over tropical Asia. It had arrived in Krakatau by 1919, but I have not heard of it from any other island.

Rubus (*Rosaceae*).—The blackberries and raspberries form a genus which is extremely widespread, extending practically all over the world. The plants, however, are most abundant in the temperate regions and scanty in the tropical regions, though by no means scarce there. They possess the great advantage of being able to thrive in the coldest parts of the world, as far north as any plants go, and are equally at home in the tropics down to the Equator. The shrubs are usually scandent or sarmentose in temperate and tropical regions, but reduced to simple erect shrublets in the Arctic regions, R. *chamaemorus*, R. *saxatilis*, and R. *illicebrosus*, of Japan, while the Chilian species are creepers. In open country they usually form rather dense thickets or masses climbing over other shrubs, but I have seen R. *Hasskarli* in dense forest, climbing on trees, in the Malay Peninsula.

The fruits are a mass of achenes covered with a sweet juicy pulp, borne on a conical—or more or less flattened—spongy receptacle. The achenes vary in size and number, and, as a rule, the fewer they are, the larger they are. They are black, pink, or yellow-orange in colour, and usually quite conspicuous.

These plants are extremely popular with birds, and I have a list of 43 birds known to feed on them, but these are only of the north temperate zone, as no observations have been made on the kinds of birds which eat them in tropical or southern countries. I may say, however, that having brought from the mountains of the Malay Peninsula plants of the beautiful *Rubus rosaefolius*, a species very widely distributed over the mountains of India, Java, Sumatra, Borneo, Celebes, New Guinea and the Philippines, and East

Australia, and planted them in the Botanic Ga[illegible] Singapore, I found the whole crop of fruit eaten by birds as soon as it [illegible], probably by bulbuls. Being an attractive plant, both in its flowers and fruits, it has been planted and allowed to run wild in the West Indies, Porto Rico, San Domingo, etc., and in South America, about Rio de Janeiro, also St. Helena and Mauritius, where it was introduced from the Malay Islands by Commerson in 1742. Many of these alien plants are the double-flowered form of garden origin, showing that they are not natives of the country.

Though the plant only occurs wild in the Malayan mountains at 4,000 or 5,000 feet altitude, it also apparently thrives very well in lowland stations when introduced. The fruit is in the shape of a large raspberry, and is of the same bright pink colour, and, as it stands up well, is very conspicuous and attractive to birds.

Besides birds, the fruits of *Rubi* are eaten by a few mammals, marten-cats, bears, etc., but I do not think they owe anything of their wide distribution to bats, as the plants are always strongly armed with hooked thorns, and the bats would be afraid of approaching them, as they would get their wings entangled and torn. Indeed, the Malays often protect their fruits from raids of bats by tying to the bunches the whips (*flagella*) of rattans, similarly armed with hooked thorns, which entangle the bats and tear the membrane of the wings.

Rubi are found in many islands, in Polynesia, Hawaii, the Azores, Canaries, Madeira, and a species has been recently recorded from Ascension Island, but Hemsley believes it to be an introduced plant. They are absent, however, from most oceanic islands, Christmas Island, Fernando de Noronha, Krakatau, Juan Fernandez, the Admiralty Isles, Kerguelen and the other Antarctic islands; Bermudas, Mauritius, Seychelles, St. Helena (though 3 or 4 species have been introduced into the last-mentioned islands and have run wild). The English blackberry, introduced into New Zealand, has become a pest, spreading everywhere, partly by its sarmentose rooting branches, and partly by the aid of birds. The absence of the *Rubi* from tropical Asiatic remote islands is probably due to the fact that most of the species inhabiting India and Malaya are inland and mountain species, far away from the sea-coast.

The *Rubi* first appear in the Reuverian beds (Pliocene), and the common English blackberry as early as the Cromerian beds, a little later.

Climbers.—The Ivy (*Hedera helix*) is very well known as a source of food-supply to birds, who disseminate the seeds. It belongs to the order *Araliaceae*, of which almost all the species are shrubs, often epiphytic at first, or small to medium-sized trees, and are very abundant in the tropics. Far the greater number of species have small black berries, sometimes very conspicuous, a few have green or grey berries, and a small number of epiphytic ones yellow or red. One species of *Heptapleurum* reached Christmas Island. It is endemic, but allied to a species with yellow berries. I have never seen the fruits of it.

The Ivy is by far the most widely distributed of any species in the order, ranging all over the north temperate region in both hemispheres, and into the Canary Islands. It is known to have been a native of England in the Inter-glacial period. In England it flowers late in the autumn, and its fruits ripen through the winter, being quite ripe at the nesting period of our earlier birds, when it is greedily eaten by blackbirds, thrush, wood-pigeon, corn-bunting and other birds. The blackbirds, as is often their wont when berries are abundant, eat a large number of the fruits and disgorge the seeds at some distance from the plant, only swallowing the pulp. I have seen a large number of these seeds, or, more correctly, pyrenes, lying on the side of a nest, where doubtless the pulp had been used to feed the young. In such abundance are they to be found, that during the war with Germany they attracted the

notice of certain people, who, struck by their curious appearance, sent them to the Royal Gardens, Kew, as suspected poisonous sweets dropped from German aeroplanes. The pyrenes are from 3 to 5 in number, and, when freed of pulp, are pink in colour, from the pink pulp which surrounds them.

Miss E. L. Turner (in "Broadland Birds," p. 3) writes of the Corn-bunting (*Emberiza miliaris*) feeding its young:—"About twice a day ivy berries were "administered. I have seen thrushes and blackbirds feed their nestlings with "these berries, but never more than twice during the day. It would seem as "if the fruit must possess some virtue which in small doses is good for "nestlings."

It must be remembered, however, that there is very little fruit of any kind usually left on the plants after the winter, and the ivy is the only abundant one. If, as is probable, the young birds require some amount of vegetable food in addition to their animal food, this is almost the only suitable source. In the case of the corn-bunting, the dry grains and seeds the adult usually lives on would not be suitable for the digestion of young birds, and ivy berries would serve as a substitute.

The most common species of *Erycibe* (*Convolvulaceae*) is *E. Princei* Wall., which occurs all over the Malay Peninsula. It produces large panicles of drupes, at first orange, then turning black. It occurs in open thickets, and is very conspicuous. The unripe orange drupes set off the ripe showy black ones, as the fruits do not all ripen at once. The contrast of the bright-coloured unripe fruit with another coloured ripe fruit is a very common way of attracting the notice of birds in search of fruits. Most of these *Erycibes* have dull grey or brown fruits, and are very local, but *E. Princei* Wall. extends its range to Sumatra and Borneo. The next species most common is *E. malaccensis*, in which the fruits change from orange to purple, but it is not so common nor so widely spread as *E. Princei*.

Another open-country climber is the little Passion-flower with small black grape-like fruit (*Passiflora minima*). The fruits are about ¼ inch through, pulpy and sweet. I found some plants of this at the foot of a large fig tree in the Botanic Gardens, Singapore, where it was certainly never planted, but brought by some bird, probably by bulbuls, which haunted the tree. It had obviously been at one time introduced as an ornamental plant, but, except for the bird-planted ones, had elsewhere disappeared.

Vitis (*Ampelideae*).—This order, with sweet juicy berries, very popular with birds, consists entirely of climbing plants except one genus *Leea*, in which the plants are shrubs of tropical Asia, but which are also bird-dispersed. The climbing species are divided up into a number of very closely allied and almost indistinguishable genera (except the genus *Pterisanthes*), and are spread over all the warmer parts of the globe. Only one species occurs in Europe, *Vitis vinifera*, the origin of the grape, which certainly appears in the Pliocene beds, preceded by several others, some as early as the lower Miocene, but all vines disappear about the Glacial period from Britain. They are more abundant in North America, and very abundant in the tropics of both worlds. Species of *Vitis* occur in the islands of Fernando de Noronha, Christmas Island, Bermudas, Krakatau, but vines are absent from Madeira, the Canaries and Azores, Juan Fernandez, Kerguelen, and all Southern Atlantic islands.

The berries of these plants (including all the genera formerly included under *Vitis and Cissus*) are black, white, more rarely red, pink, or yellow, and contain a few small seeds.

They are eaten greedily by birds, chiefly thrushes, starlings, and small birds. I have recorded 18 species of birds which feed on them, but these are chiefly from North America and Europe. There must be very many birds which eat those of the tropical regions, which have not been recorded.

Their absence from some of the islands mentioned is perhaps due to the want of forest trees for them to climb on, as they are always woodland or hedge plants, and the limited diffusion of the small-sized birds which alone eat them, and, in the case of the Atlantic islands, the unsuitability of climate accounts for their absence.

White Fruits.

White drupes and berries, especially of open-country plants, are by no means rare, but are mainly confined to shrublets, bushes and low climbers, comparatively rare in herbs and trees over 20 feet tall. Two of the herbs with white fruit are of considerable interest. The genus *Hedyotis* (*Rubiaceae*) comprises a large number of weedy herbs growing along waysides, open sandy spots and exposed mountain-tops, and their fruit consists of a pair of very small, slightly woody cocci containing a number of minute black seeds released by the dehiscence of the cocci and dispersed by wind and rain-wash. Only one species, *H. congesta*, frequents jungle, and is adapted for a life in the shady forest, where rain and wind would not assist in the dispersal of the seeds. It is a tall stout plant, with the usual axillary clusters of small white flowers characteristic of most lowland species, but the cocci, when ripe, become white, fleshy and sweet, 0·15 inch long, and do not dehisce, but are quite suitable for dispersal by the small birds which fly low in the forest. It is widely distributed and common from Mergui, the Nicobar Islands, Malay Peninsula and islands to the Philippines.

Gomphostemma is a genus of *Labiatae* occurring in the jungles of Burma, and the Malay Peninsula and islands, and is the only genus of the order occurring in thick forest in the Malay area. The other *Labiatae* possess, as fruit, 4 little dry nutlets, which are usually shaken out of the calyx by wind and further dispersed by rain-wash. In *Gomphostemma* the nutlets are white and drupaceous, and sufficiently conspicuous to be seen by small birds seeking food. They are evidently adapted for that purpose.

Another herb with conspicuous, white, succulent berries is *Campanumaea celebica* Bl., a straggling herb growing on exposed banks in mountains in India, Malaya and China; and among the *Scitamineae* we have some tall species of *Alpinia*, *A. scabra*, with large erect panicles of small, round white fruits, conspicuous in the lighter parts of the mountain forest; the tall Marantaceous *Donax grandis*, with pendulous racemes of round, white 1-seeded fruits, with very little pulp surrounding the seeds, common in open woods in the Malay forests; and *Elettariopsis longituba* (*Zingiberaceae*), with long prostrate racemes lying in wet mud in dense forests, with white capsules containing numerous seeds in an aromatic pulp. There are many other Gingers like this last species which have the fruit lying close to the ground, but usually bright red, and too large for the food of small birds. I imagine this white and red colouring serves to attract the attention of the ground game, pheasants, etc., but it may possibly also attract wild pigs, tapirs, and other such animals.

Actaea alba, of North America and Japan, is a herb with a dense panicle of white fruits. Closely allied forms have bright red fruits, and these species or forms seem much commoner than the black-fruited *A. spicata* of Europe. *Dianella revoluta* (*Liliaceae*) is another herb with white (often blue) fruits.

Low Shrubs and Shrublets.—Very conspicuous in the open sandy woods of the Malay Peninsula is the beautiful unbranched shrublet *Euthemis leucocarpa* (*Ochnaceae*), with a showy raceme of white (more rarely rose-pink or scarlet) berries ¼ inch through, while in the denser wet jungle we have *Adenosacme malayana* (*Rubiaceae*), a shrublet about 2 feet tall, with white translucent berries; and *Chloranthus officinalis* (*Chloranthaceae*), a low shrublet with very similar

fruit. (Another less common species inhabiting mountains has bright red fruits.)

Callicarpa longifolia (*Verbenaceae*), an open-country and roadside shrub about 5 feet tall, has axillary cymes of very small white drupes. The other species of the genus have purple or black fruits, often very showy, but this white-fruited species has by far the widest distribution, and is, indeed, the most common species occurring in India, all over the Malay region, North Australia and in Christmas Island, where, as it was found in the first visit there by Lister, it was undoubtedly brought by birds.

Climbers.—A few slender climbers, usually occurring in open woods or more frequently on hedges and open village spaces, have white fruit. *Vitis carnosa* (*Ampelideae*) is a common vine in open places, hedges, etc., in the Malay region, which has a corymb of small white grapes, ¼ inch through. It occurs in India, Cochin-China, the Malay regions, and appeared in Krakatau in 1906.

V. cantoniensis is another vine of waste ground which has white grapes, and is fairly abundant in China, Cochin-China and the Malay Peninsula.

Cyclea laxiflora (*Menispermaceae*) is another slender climber with white drupes, common in hedgerows, but also occurring in mountain forests in the Malay Peninsula.

Psychotria sarmentosa (*Rubiaceae*) is a conspicuous climber with small, white 2-seeded drupes, on hedgerows and over bushes in open country in the Malay Peninsula, and a variety of it occurs in open places on the high mountains. *P. obovata*, very similar in appearance, is also a common hedgerow plant. It is rather remarkable that while the erect shrubby *Psychotrias* of the Malay Peninsula have always red or orange fruits, all the climbing ones, *P. obovata*, *P. sarmentosa*, *P. Cantleyi*, *P. ovoidea*, *P. Maingayi*, and *P. Ridleyi*, have pulpy and rather large white fruits. Except the first two, these white-fruited ones grow in rather open parts of the forests near the edge, and climb a short way only up the tree trunks, or creep on the ground.

Trees and Tall Bushes.—*Ardisia* (*Pimelandra*) *Wallichii* (*Myrsineae*) belongs to a section of the large genus *Ardisia*, which, unlike most of the species, bears the fruit on the stem (not on terminal or subterminal panicles, in which cases the fruit is red), and has white drupes as big as a pea. It is a small tree or shrub occurring in dense dark forest in the Malay region.

Aglaia glabrifolia (*Meliaceae*), a bushy tree about 10 feet high, or large shrub, has also white fruit showing out clearly against the deep green leaves.

Fluggea microcarpa is a common little Euphorbiaceous bush which, when the small white berries are ripe, is very handsome, some being covered all over with the conspicuous fruit. It grows very abundantly in open country and along river banks in the Malay Peninsula and islands, as well as Africa, India to Australia, but is replaced in Ceylon by *F. leucopyrus*, which chiefly differs in being spiny. One cannot doubt that this pretty shrub owes its wide distribution largely to its showy fruit.

Eugenia zeylanica (*Myrtaceae*), a shrub or small tree about 30 feet tall, has white, pithy, sweet, aromatic drupes, ¾ inch long, often very conspicuous, especially in the bushy form. It is common and widely distributed in open country and by rivers in the Malay region.

Symphoricarpus racemosus (*Caprifoliaceae*).—The Snowball shrub is an American plant cultivated in shrubberies in England and elsewhere for its large round conspicuous white berries which are ripe in the autumn when the leaves begin to fall. They are soft and juicy. They are not very popular with birds here, though blackbirds and pheasants eat them. In America, however, they seem to be very popular with many birds. The blackbirds usually suck the

juice out of the berry, leaving the skin. I have very seldom seen seedlings away from a bush, and it seems to reproduce itself in England very little. I found one seedling in a Yew bush in company with an Elder (*Sambucus nigra*) and *Mahonia aquifolium*, all obviously brought by blackbirds. The fruits in England, however, seem to be mostly seedless, which probably accounts for this scarcity.

The low forest shrubs *Lasianthus* (*Rubiaceae*), of the Indian and Malayan regions, have often white pulpy fruits, but more commonly they are blue. In the same way we often see white fruits of *Dianella* and *Dichroa*, in which plants they are usually blue.

The parasitic Mistletoes, *Viscum* and *Phoradendron*, have also white succulent fruits, an account of which, however, is given elsewhere, in a section dealing with *Loranthaceae* generally, pp. 468, 474.

Cassytha filiformis is a parasitic, leafless, yellow plant, generally referred to the *Laurineae*, which grows parasitically on bushes on the sea-shores of Indo-Malaya, and reached Krakatau in 1897. The fruits are white and pulpy. Guppy has shown (" Naturalist in the Pacific," p. 52) that the fruits are buoyant and can be dispersed by sea-currents, but they have been found in the crop of pigeons. *Cestrum aurantiacum* is a lofty climber from South America with white fruits.

Sloetia sideroxylon (*Urticaceae*) is a Malayan tree attaining a very large size, though it often fruits when only 12 or 15 feet tall. The fruit is borne in axillary catkins, of which the greater number of flowers are males, with only 2 or 3 female ones at the base. The small globose white nut is half enclosed in the 4 sepals of the female flower, which, when ripe, are swollen, pulpy, succulent, sweet and white, and tolerably conspicuous. When a bird attempts to bite the juicy sepals, the fruit is shot out suddenly to some distance, and, being round, rolls along. It is probable that the continued swelling of the sepals may eject the fruit without the aid of a bird, but the rather conspicuous white colouring and sweetness suggest that the birds play some part in dispersing this fruit.

Villebrunnea sylvatica is another *Urticaceous* tree in which the fruit is white. It is borne in small heads, and the minute achenes are adnate to the perianth, which becomes fleshy and white. The whole fruit-head is only about $\frac{1}{10}$ inch across, but they are very abundant on the tree when it is in fruit, and are thus sufficiently conspicuous. The tree is about 50 feet tall, with a bushy top, and is found on open edges of forests in the Malay Peninsula, Sumatra and Java.

Blue Fruits and Seeds.

Blue is rather a scarce colour in plants, whether in the flowers or fruits, in comparison with other colours, and it is particularly uncommon in tropical regions.

In some cases of blue fruit the colouring is due to a waxy blue bloom overspreading the berry as in *Mahonias*, and some *Vacciniums*, and the flowering Currant (*Ribes sanguinea*). This blue bloom serves to lighten up the dark, inconspicuous, blackish colour against the foliage, and undoubtedly shows off the fruits, many of which are popular with birds.

But sometimes we get fruits in which the pericarp takes on a fine blue colour, as in *Dichroa* (*Saxifragaceae*), and *Dianella* (*Liliaceae*), which usually have bright azure berries, although in some forms (usually those with white and not blue flowers) the berries are white. The former is a shrub inhabiting light open woods in India and Malaya; *Dianella* is a tall herb found in open places, heaths and shores, chiefly in Australia; I have fully described it under the account of the transformation of capsules to berries (p. 422), and shown

that it owes its distribution, as the widest spread of any genus in the section *Anthericeae*, to its transformation into a bird-dispersed plant.

The genera *Lasianthus*, *Saprosma*, *Amaracarpus* and *Cephaelis* (*Rubiaceae*) are low shrubs, usually about 2 or 3 feet tall, occurring in dense forest. *Lasianthus* has often white, more frequently light to dark blue, rarely black, 2- to 4-seeded pulpy fruits about ¼ inch long, solitary or 2 together in the leaf axils. *Cephaelis* has fruits, usually azure blue, in a head, and those of *Gaertnera grisea* (*Loganiaceae*) are similarly coloured; one *Cephaelis* has the fruits black. The colour is usually not very conspicuous in the dark shadows, interspersed with gleams of sunshine in the forest, but would be conspicuous enough to low-flying forest birds, ground-doves, pheasants and such birds.

A few trees have blue or bluish fruits, e.g., *Elaeocarpus Ganitrus* and some other species, *Symplocos fasciculatus* and *Eugenia acuminatissima*, a tall tree with blue-purple fruits, and a few climbers, *Dissochaeta gracilis* (*Melastomaceae*), but the trees have drupes largely dispersed by bats and monkeys, and the blue colour is by no means sufficiently bright to be attractive from a distance.

One or two of the shrubby herbs, *Labisia* (*Myrsineae*), have light blue drupes. The species is scarce (*L. longistylis*), and a mountain plant. The common low-country species, *L. pothoina*, has very showy red drupes.

One of the most beautiful blue-berried plants is *Psychotria cyanococca*, of Nicaragua, which was introduced as an ornamental plant many years ago by Seemann. It seems to have quite disappeared from cultivation, and, indeed, not to have been seen again. The berries, about as large as peas, but more elliptic, form a considerable mass like a small bunch of grapes, of a beautiful indigo-blue, hanging from an axillary peduncle below the leaves, and each containing the characteristic 2 seeds, flattened on one side and ribbed on the rounded back. The plant is a low shrub, or perhaps a herb. It is interesting as it appears to be the only blue-fruited *Psychotria*, all the rest having red, orange, or white berries.

Another showy plant from its blue berries is *Pollia thyrsiflora* (*Commelinaceae*), a stout herb from 1 to nearly 2 feet tall, common in damp, fairly open spots in the Malay Peninsula and Archipelago, and the Andaman Islands. It has a thyrsoid dense panicle of bright, dark steel-blue ellipsoid fruits. Of these, the outside is crustaceous and contains a number of small seeds. The fruit is quite dry, and there seems very little in it to tempt any bird or animal. *P. sorzogonensis*, with a lax panicle, has similar rather larger light blue fruits, but most of these *Commelinaceae* have grey or lead-coloured fruits. The capsule, for such it must be called, being very dry, dehisces irregularly. I have little doubt that birds do disperse these plants, and it is noticeable that the ones with conspicuously blue fruits are the most widely distributed and common species. *P. sorzogonensis* occurs in India, China, the Malay Peninsula and islands, and New Caledonia.

One interesting genus in which the seeds are blue is *Peliosanthes* (*Liliaceae*), low herbs inhabiting jungle in the Malay regions and India. In these plants the capsule splits and almost disappears when the fruit is very young, and the seeds, usually 1, more rarely 2, develop outside the remains of the pericarp. They are oblong and, when ripe, about ½ an inch long. At first dark green, they eventually become azure-blue and very conspicuous. The blue portion is the thickened soft and eatable testa. They are certainly removed, very soon after ripening, by some animal or bird, but I have no evidence as to what it is. A similar case is that of *Caulophyllum divaricatum* (*Berberidaceae*), a woodland herb of North America known as the Blue Cohosh. Here, too, the capsule splits very early, the seeds develop outside the withered ovary, and have a fleshy blue testa, as in *Peliosanthes*.

It is very rare for blue to be combined with any other colour in fruits.

The only cases I know are those of the beautiful *Clerodendron Bethuneanum* (*Verbenaceae*), of Borneo, in which the pulpy dark blue fruit is surrounded by the enlarged red sepals, and the duller blue fruits of *C. Fargesii* also surrounded with stellate red sepals, and *Phoebe macrophylla* (*see* p. 416).

Fruit Coloration and Foliage.

Kerner urges that the particular colour assumed by fruits and seeds at the time of maturity varies according to that of the foliage by which they are surrounded. The different tones of red stand out best from a green environment, therefore for plants with evergreen foliage a red coloration is the most advantageous. On the other hand, red fruits would stand out but little against a background of foliage that had donned red or yellow tints of autumn by the time they had ripened, and accordingly the fruit of *Ampelopsis hederacea*, *Cornus sanguinea*, etc., are black.

There is a certain amount of truth in this, but there are many exceptions. Thus in the *Euonymi*, *E. planipes*, *E. oxyphyllus*, *E. verrucosus*, and some forms of *E. europaeus* and *Crataegus coccineus*, and some other of the American species, the leaves in autumn are of a magnificent red or orange. While the fruits are equally orange or red, and certainly not so visible as they would have been if the leaves retained their green colour, yet I observed that the birds detected the fruits and devoured them very speedily. I have seen blackbirds greedily devouring the black inconspicuous berries of *Cotoneaster Wallichii* almost hidden in the green foliage, in preference to the scarlet berries of the red-fruited *Cotoneaster* close by. Red or black fruits in corymbs or panicles are certainly more conspicuous than isolated or shortly-racemed fruits, yet half-hidden drupes of the Holly are devoured entirely before those of *Pyracantha*. The very conspicuous white berries of *Symphoricarpus* seem to attract birds in England but little, and I have rarely seen birds eating them, or found bird-dispersed seedlings.

The fall of the leaves in deciduous plants is very advantageous to dispersal, as the fruits are most conspicuous when the trees are bare, and isolated trees with brilliantly-coloured fruits are more speedily cleared than crowded trees.

The beautiful American Winter-berry (*Ilex verticillata*) is deciduous and extremely showy when the leaves have fallen and the scarlet fruit ripe. The fruits are quickly attacked by birds, chiefly thrushes and blackbirds, but I have seen thrushes, missel-thrush and blackbirds busily engaged in eating the inconspicuous fruits of the Hackberry (*Celtis occidentalis*), and quite neglecting the juicy scarlet fruit of the *Ilex* which grew close to it; in fact, though the sweet juicy berries of the Rowan tree, *Ilex verticillata*, *Cotoneaster Wallichii*, and Yew are very popular and much sought after, the firm-fleshed, rather dry fruits of *Crataegus oxyacantha*, *Pyracantha* and *Celtis* seem to to be nearly as popular when the birds want something more solid to eat.

In the tropics, e.g., the Malay Peninsula, few of the trees are deciduous, and when they do, for a few days, shed their leaves, they are usually without fruit. The *Cinnamon* (*C. iners*), which becomes nearly or quite bare of leaves, does not begin to flower till after the appearance of the fresh leaves, and does not produce its black fruits till the leaves are firm and green. But most of the trees of the tropical rain-forest are evergreen, and even if the fruit is produced in abundance, it is not common for it to be produced in large panicles or corymbs—at least, in the case of coloured drupes or berries. In such cases as *Ilex cymosa* and *I. macrophylla*, where the little red fruits are borne in fair-sized corymbs, the whole mass does not ripen at once, but only a few are fully ripe at a time, and we have there nothing corresponding to the showy panicles of the Rowan tree or *Pyracantha*. There are no seasons in these regions, and flowering and fruiting for the most part go on throughout the year, though not entirely, for it is generally considered that, as regards cultivated tree-

fruits, there are two fruiting seasons. When fruit is abundant, some trees fruit in the forest once or twice a year, others at longer intervals, and some not once in many years. The smaller trees and shrubs, which supply most of the bird-food, usually fruit a little all through the year. I may instance the difference between countries with a periodic dry season and those like the tropical rain-forest area, where there are no regular seasons, by using the Cotton plant as an example. In countries like Brazil or India, where there are periodic dry spells and periodic rains, the cotton pods all ripen at once, so that the whole year's crop is gathered in a few weeks. In Singapore, as there was no dry season, the cotton flowered and fruited all through the year, so that collecting the crop had to be done weekly, for the greater part of the year, only a few pods at a time being ripe on the bushes. In the same way the fruit-eating birds in the rain-forest region, though able to procure some kind of fruit all the year round, have to fly far and seek widely for their food.

Occasionally a climber or tree has a more or less fixed period for fruiting. Thus *Trichosanthes* (*Cucurbitaceae*) has large, egg-shaped crimson fruits, usually ripe in the early months. They are beloved of the Jungle Crow (*Corvus enca*), which only appeared in Singapore when these fruits were ripe. When a tree of *Ficus benjamina* or *F. retusa* is covered with the small, inconspicuous, purple-black figs, myriads of bulbuls (*Pycnonotus*) and often Glossy starlings (*Calornis chalybaea*), and Green pigeons (*Treron vernans*), and many other fruit-eating birds appear, and devour the fruit all day, and are often attacked by hawks. During the night these birds are replaced by fruit-bats (*Pteropus* and *Cynopterus*), who also feed on the figs. When all the fruit is finished, the birds and bats disappear, and doubtless carry the seeds to considerable distances.

There is no doubt that sweet and juicy berries or drupes are taken most readily by birds. In England the berries of the Rowan tree (*Pyrus aucuparia*), and the juicy arilled fruit of the Yew (*Taxus baccata*) are taken first—in fact, the trees are cleared almost immediately the fruit is ripe. The blackbirds ate the fruit of a Rowan tree in my garden before they were actually ripe on one occasion when the weather was very dry. The juicy but acid fruits of *Hippophae rhamnoides*, the Sea Buckthorn, and of most species of *Berberis*, *B. Wilsoniana*, *B. subcaulialata* and *B. vulgaris*, are usually not eaten at all by birds in Kew Gardens, not even when the birds are hard put to it by snow and frost, though I have seen a blackbird eating the berries of *B. vulgaris*. The rather dry fruits of *Cotoneaster rotundifolia*, *Pyracantha angustifolia*, *P. crenulata*, are also much neglected here, though *P. coccinea*, perhaps a little softer-fleshed, is altogether cleared before the winter is over, so that at Kew it is necessary to net the bushes to preserve the fruit. Doubtless in the natural habitats of these brilliant-fruited bushes the fruits are eaten by some birds, but the English birds eat but little of them.

Mixed Coloured Fruits.

Another system of bird attraction is formed by the fruits, as they ripen, passing through different colour stages, so that, as all do not ripen at once, the panicle, corymb, or spike show a mixture of colours, the unripe ones, usually red or sometimes white, calling the bird's attention to the less conspicuous ripe black fruit.

In some of the Cornels (*Cornus* sp.) the young fruits become red and, when ripe, black. The bird, going to investigate the red-fruited corymb, finds and swallows the little black drupes. But the finest example of this method is that of *Viburnum lantana*, the wayfaring tree of the English chalky districts. In the autumn the whole corymb of fruit, as much as 6 inches across, is of a magnificent red. When the fruits are quite ripe, the pulp becomes juicy and sweet, and the whole fruit black. The birds, chiefly blackbirds and thrushes, are attracted by the splendour of the unripe fruits, but only eat the black

ripe ones. As the fruits ripen slowly, 1 or 2 on a corymb at a time, the birds renew their visit day after day till gradually they have eaten all, as they become black and ripe. This takes a week or more. In this way the seeds are more widely dispersed than in the case of the Rowan tree, or *Pyracantha*, where practically all the red fruits are ripe at once, eaten and disseminated more or less *en bloc*.

Another form of mixed colouring, by the change of the colour of the fruits as they ripen, is to be seen in the elegant forest Palms, *Iguanura*, of the Malay forests. These are dwarf Palms with a terminal tuft of obcuneate or pinnate leaves, below which depend simple or panicled slender spikes 1 foot or more long, with small flowers embedded in them. The fruit is oblong, and first appears about ½ inch long, white; it then turns bright red, and finally, when ripe, black. As they ripen at different times, you may see white, red and black on the same spike. The white is especially conspicuous in the dark forest. The birds apparently do not take either the white or red fruits, but the black vanish so fast that it is difficult to secure ripe seed.

COLOURED PANICLE OR CYME BRANCHES.

In many plants of various orders we find in the fruiting stage that the branches of the raceme, cyme, or panicle, are usually coloured red so as to increase the brilliancy of the infructescence and attract the attention of birds a considerable distance away. In some cases, e.g., *Clerodendron fallax*, the whole inflorescence, branches, flowers and all, are bright red. The red colouring here serves primarily to add an attraction to insects for the pollination of the flowers, rendering the whole inflorescence more widely conspicuous from a distance than it would otherwise have been. After the flowers have fallen, the colour still remains as bright, and sets off the small black drupes, which would otherwise not be very conspicuous.

In *Pogonanthera pulverulenta* (*Melastomaceae*), a shrub with panicles of small white flowers, epiphytic on high trees or frequently growing on rocks, the branches of the inflorescence are red to set off the white flowers, and, remaining red, serve to call attention of birds to its small red berries. As this plant is usually an epiphyte, and has very small flowers, it also possesses small drupes which would be inconspicuous for birds to detect the infructescence not coloured. Several of the *Medinillas*, also epiphytic *Melastomaceae*, have a similar arrangement. In *M. Scortechinii* the whole inflorescence and fruit are cherry-red, and in *M. Hasseltii* they are orange-scarlet. These all inhabit the dense forests of the Malay Peninsula, and are very conspicuous in fruit from the brightly-coloured cyme-branches.

In other cases the panicle- or corymb-branches take on a red colour, while the ripe fruit has a contrasting colour. The Laurineous tree, *Phoebe macrophylla*, has large spreading panicles, which swell and become bright red in the fruiting stage, and the drupes, about 1 inch long, are dark blue (Pl. XV, fig. 7). It is a native of the Malay Peninsula. In many of the *Ixoras* the panicle branches take on a red colour when bearing their globose black or steel-grey drupes.

Cornus Bretschneideri (*Cornaceae*) a native of China, has very small black drupes borne on a corymb, which takes on a red colour as the drupes ripen.

Among the Palms, especially in the genera *Pinanga* and *Nenga*, of the Indo-Malayan forests, the inflorescence, which consists of a number of stout, flattened spikes clustered on a short stalk and hanging down beneath the leaves, becomes of a brilliant red, and shows off the black olive-like fruits conspicuously. *P. malayana*, of the Malay jungles, is remarkably attractive in fruit; the rachis of each spike is much thickened as the fruits ripen, and is 6 inches long and ½ inch in width. The *Chamaedoreas*, of the Amazons forests, have a somewhat

similar arrangement. All these Palms are dwarf, only some 10 feet or more tall, so that the bright rachis makes it conspicuous a long way off. In such Palms as have red fruits the rachis is not coloured, as the spadix is conspicuous enough when the fruits are ripe.

A very singular plant is the Malay Caterpillar Vine (*Pterisanthes*), of which there are 4 or 5 species in Malay and Borneo. These vines are very slender, and bear on the end of a filiform peduncle a flat, simple or lobed, more or less undulate rachis, about 5 inches long and $1\frac{1}{2}$ inches wide, oblong in outline. On this, which when in flower is green, are a number of small yellow bi-sexual flowers sunk in the rachis, and along the edge a number of stalked female or neuter flowers. When the fruit is ripe, the rachis becomes bright red and conspicuous, the small grapes being black. These vines are evidently derived from a species of *Ampelocissus*, in which genus the inflorescence consists of a sometimes branched spike of small flowers. A connecting link is a species I found in Borneo with distinctly flattened spikes and sessile flowers. The large showy flat red rachis of *Pterisanthes* is a great improvement on this plant and its allies, from a dispersal point of view.

Chasalia curviflora (*Rubiaceae*) is a dwarf shrub about 2 feet tall, with a number of flowers in a short terminal cyme, on short slender pedicels. Only a few of these, however, develop fruit. During the formation of the berry the peduncle and 2 (rarely more) of the branches of the cyme enlarge and thicken, becoming fleshy and white, or occasionally, in cases where the whole plant has taken on a purple hue, of a rose colour. The berries are pulpy and shining black, containing 2 plano-convex pyrenes (Pl. XV, fig. 5).

The thick, white pulpy branches and the contrasting black berries make it very conspicuous in fruit, and it is doubtless due to this that it is much the widest distributed and most common species in India, Ceylon, the Malay Peninsula and islands. There are 3 other species in the Malay Peninsula which are very local, and the only one I have seen in fruit, *C. minor*, has black fruits, but they are not at all so conspicuous, as the peduncle and branches of the cyme are not thickened or white as they are in the common species.

Enlarged and Coloured Pedicels.—In a number of plants the fruit-stalk or pedicel becomes enlarged, fleshy and coloured. In the flower stage it is often small and not at all thick. As the drupe enlarges, however, the pedicel continues to grow in length and thickness, and usually becomes of a conspicuous red. This is attractive to birds, which carry it off and with it the drupe, which (it is probable) they swallow in many cases. The genus *Dehaasia* (*Laurineae*), Indo-Malayan bushes and trees, possess fruits of this nature. The most showy of them is *D. microcarpa* Bl. (I really think Blume must have meant *macrocarpa*, as it has the biggest and handsomest fruit of any.) Its flowers, stalk and all, are only about $\frac{1}{12}$ inch long. The fruit is a black drupe, oblong, 1 inch long, on a rather longer peduncle of a brilliant red. It is not at all rare in forests, a tree 40 feet tall, all over the Malay Peninsula, Java, Sumatra, and Borneo. From the great size of the fruits I conclude it must be dispersed by hornbills and fruit-pigeons. Some species of the allied genus *Alseodaphne*, viz., *A. peduncularis* and *A. Wrayi*, have very similar fruit. The former is a small tree or shrub up to 12 feet tall, common all over the Malayan forests.

In the genus *Podocarpus* (*Taxaceae*) the seed is borne on a fleshy peduncle, or short branch with suppressed leaves. This peduncle, though frequently plain green or grey-green, in many species becomes of a bright red, contrasting with the grey or black seed. The ovule in this case is borne in the axil of one of the small leaves. The red peduncle is the attractive part to birds. *P. latifolius*, of South Africa, has one or two blue-black seeds borne on a double semi-ovate connate red peduncle, broader than the drupe. Marloth

says it is attractive to starlings and other birds. The genus, which is entirely tropical or subtropical, is of very wide distribution, occurring in India, Malaya, Australia, Fiji, New Zealand, Africa and Madagascar, South America from Venezuela to Chile, and the West Indies.

The *Taxaceae* do not appear to be known earlier than the Cretaceous period, but both this genus and *Taxus* are far more widely distributed now than the *Araucariae* and *Cupressineae* of the Jurassic period. It is undoubtedly due to their dispersal by birds that they are so widely distributed.

Coloured Bracts.—Coloured bracts in fruit to attract the attention of birds are not very common. *Lonicera Ledeboeri* (*Caprifoliaceae*), a shrub honeysuckle of California, however, possesses a pair of rounded bracts forming a kind of cup surrounding 2 sessile flowers. When the flowers have fallen, these bracts become larger, and spread out flatter, taking on a deeper red tint, so as to contrast with the oblong juicy, shining black drupes (Pl. XV, fig. 1). Coloured bracts and bracteoles in a dense head, setting off first the white flowers, then the black fruit, are to be found in *Clerodendron deflexum* (*Verbenaceae*), which is more fully treated under Coloured Sepals.

Coloured Sepals.—The sepals of flowers are often coloured brightly to form a contrast with the petals, so as to be more conspicuous to pollinating insects. In many cases, after the flower is fertilised, the coloration of the sepals is no longer necessary, and the sepals either fall off, or the colour disappears; but if the fruit is a drupe or berry, and intended for the food of birds, the sepals retain, and often increase, their colour, becoming at the same time larger and more conspicuous, nor is it rare for the sepals, inconspicuous and of dull colour in the flower, to develop into larger and gaily-coloured organs. In these cases the predominant colour in calyx coloration is red, and the drupe or berry black.

The genus *Clerodendron* (*Verbenaceae*) comprises a large number of shrubby herbs, bushes, or small trees, abundant in open country and woodland all over the tropical parts of Africa and Asia, and more scantily in tropical America. The flowers are in loose or compact panicles, and the fruit a drupe of 4 pyrenes with usually juicy, pulpy, black pericarp. In many of these the calyx becomes larger and often spreads in a star, usually red, while the fruit is black or blue. *C. siphonanthus*, *C. disparifolium*, *C. penduliflorum*, *C. myrmecophilum*, *C. umbratile* and other species, have red sepals with black fruit; in *C. Bethuneanum*, of Borneo, and *C. Fargesii*, of China, the fruit is blue. In this latter species the accrescent calyx is star-shaped and stiff, and I noticed in Kew Gardens the calyx acted as wings, and the whole fruit singly, or 2 together, flew about 25 yards from the tree along the grass. The leaves had all fallen when the fruit was ripe, and the bushy treelet, 6 to 8 feet tall, is conspicuously red from a distance (Pl. XV, fig. 2).

In the very common *C. villosum*, of the Malay waste ground and villages, the sepals are white and the fruit black. In *C. deflexum* the flowers are crowded into a pendent head about 2 inches wide, with numerous narrow, acute bracts and bracteoles, all, like the similar calyx-lobes, bright red. The white flowers, and the black fruit projecting from this mass of bracts and bracteoles, are equally conspicuous, the one for the pollinating insects, the other for the disseminating birds. There are other plants in which a similar modification takes place, such as in *Columnea* (*Gesneraceae*), of the Andes, in which the sepals are much enlarged and light red, and the berry globose and white.

A very curious development of the calyx for bird attraction occurs in the genera *Harmandia* and *Heisteria* (*Olacineae*), shrubs or small trees, the former Malayan and Siamese, the latter South American. The calyx of the small flowers is a minute cup, entire, or with 4 teeth. In fruiting it develops, in *Harmandia*, into a flat fleshy circular disc, 3 or 4 inches across, of a flesh-pink

PLATE XV.

BIRD-DISPERSED FRUITS.

FIG. 1.—*Lonicera Ledebouri* (fruits in connate bracts, enlarged).
,, 2.—*Clerodendron Fargesii* (fruits with stellate calyx).
,, 3.—*Melastoma polyanthum* (fruits).
,, 4.—*Sterculia rubiginosa* (reduced).
,, 5.—*Chasalia curviflora* (fruits on swollen peduncle).
,, 6.—*Scleria sumatrensis* (achene with coloured disc, enlarged).
,, 7.—*Phoebe macrophylla* (fruit panicle).

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colour, in the centre of which stands a black drupe 1½ inches long and over ½ inch through. In *Heisteria* the arrangement is similar, but in *H. coccinea* the plate is distinctly lobed. The fruits are rather smaller than in *Harmandia*, yellowish, blue or purple, the calyx-plate measures from 1 to 3 inches across, and is in some species white, in others red. The contrast between the tiny calyx in the flower and the large fleshy-coloured dish supporting the fruit is very remarkable.

Coloured Torus.—The torus or receptacle of the flower is the enlarged apex of the pedicel. In some groups it is well developed, and is especially conspicuous in the *Ochnaceae*. In the flower of *Ochna* it is small and inconspicuous, but as the fruit ripens, after the fall of the petals and stamens, it becomes large, fleshy, and bright red, and bears a variable number of black drupes, each formed of a separate pistil; they vary in number from 3 to 10. The *Ochnas* are trees or bushes of no great size, inhabiting sandy open places in Africa, India, Siam, and the north of the Malay Peninsula. The whole fruit is very showy, and no doubt attractive to birds. The allied genus *Gomphia* (*Ouratea*) has a somewhat similar structure, but the torus is not coloured, and does not attain the size of that of *Ochna*; the drupes are therefore less conspicuous, usually smaller and of a deep purple-black. They are certainly dispersed by birds, as, in the Malay Peninsula, scattered seedlings some distance from the parent tree may often be found. The genus is most abundant in South America, but also occurs in Africa, India, and the Malay Peninsula and islands.

In the genus *Scleria* (*Cyperaceae*), and a few allied genera (*Cryptangieae*), the nut, which is very small, and black or white, is borne in a cup-shaped gymnospore or torus. This is usually inconspicuous and white, but in *Scleria sumatrensis* it covers half the black nut, and is bright red. This sedge is a rough grassy plant from 3 to 20 feet long, when scrambling over bushes, and bears a terminal panicle of flowers and fruits. It is very common in the Malay Peninsula and islands, in open country. I have little doubt that the small birds eat the fruits of this plant, but have never observed them doing so. However, fruits of *Scleria* have been found in the stomachs of various birds (Pl. XV, fig. 6).

The Cashew Nut, *Anacardium occidentale*, a native of South America, is now widely scattered over the tropics, usually in sandy places by the sea. It is a large, low, much-branched tree. The fruit is a woody kidney-shaped nut, with an eatable kernel, protected, however, by a thin, black, very acrid testa. It is supported on a pear-shaped, juicy, yellow, pink-flushed body composed of the vastly enlarged torus and top of the peduncle combined. In cultivated forms the peduncle-torus is 4 inches long and 2 inches wide, very juicy, slightly astringent, but most refreshing. In the wild forms it is usually very much smaller. Introduced to the Old World from South America as a fruit tree, it has run wild in open sandy spots abundantly. There is no doubt that it owes much of its wide dispersal to human agency, though, except for its kernels, it is not very popular in the Old World, but its diffusion in countries where it has been once introduced is due to birds and also to some extent to sea-dispersal. It occurs along seashores in the Malay Peninsula, but, though the natives pick up the seeds and eat them when they find them, the plant is not cultivated. In Ceylon it is common along the seashores. Guppy doubts very much that it is sea-borne to any extent, as he states that the seeds sink very soon, but there is a very early record of germinable seed picked up on the coast of Norway, where it must have drifted. It is absent from most oceanic islands.

PART II

TRANSFORMATION OF BERRY TO CAPSULE AND VICE VERSA. THE ARIL

It has been stated by Dr. Willis that the transformation of a berry into a capsule, or a capsule into a berry, by evolution, is impossible to conceive. Nevertheless, cases do occur in which both of these phenomena have taken place, and by extremely simple methods.

It may be assumed that the evolution of the capsule is the more primitive formation of the two forms of fruit, the drupe or berry being a later development, and there is reason to believe that the 1-seeded carpel is a later stage of development than the many-seeded carpel—at all events, it is a very common occurrence. We find that for dispersal purposes we get from a many-ovuled carpel a 1-seeded fruit, the other ovules being aborted and disappearing. Attention is called to this in many parts of this work. Our knowledge of the earliest forms of flowering plants is not at present sufficient to show whether the earliest forms possessed 1-seeded or many-seeded fruits. We know, however, definitely, that a very large number of plants have numerous ovules in a carpel which may result in a many-seeded berry or in a dehiscent capsule, or a fruit in which all ovules but one are aborted, resulting in a drupe or samara, nut or 1-seeded capsule, and that this suppression of all ovules but one has a distinct relationship to the method of dispersal adopted by the plant.

The importance of the separation of the ripe seeds from one another, and their migration to some distance from each other and from the mother-plant, has been already shown, and the reduction of the ovules in a carpel to a single one is a very common way of ensuring this. The various forms of fruit which we see throughout the vegetable kingdom have been entirely evolved with a view to the dissemination of the seedlings, and owing to various changes in the environment, or to various modifications of the flower for fertilisation, it may be necessary for the plant to modify the form of its fruit for purposes of dissemination, a failure to effect which would entail, and probably has often entailed, the total disappearance of the species.

I have given throughout this work examples of the evolution of a plant or seed from a bristly wind-dispersed one into an adhesive one, the bristles, originally acting as wings, becoming hooked; of bird-dispersed fruits into winged fruits, wind-dispersed, and of these wind-dispersed fruits developing into sea-dispersed ones (*Sterculiaceae*), and so on, all due to the change of environment and of conditions of life of the plant; and here I deal with the methods of modification of berry into capsule, and of dry nucules or capsules, into bird-dispersed drupes or berries, to the great advantage of the species. As both of these transformations are due to the actions of birds, I treat of them in connection with this section. Neither forms of modification are very common, but they are very curious and interesting.

From Berry to Capsule.—*Fagraea auriculata* Jack (*F. imperialis* Miq.), of the order of *Loganiaceae*, is a large shrub, sometimes developing into a tree about 40 feet tall, with perhaps the largest flowers of any flowering plant in the world (except *Rafflesia*), being sometimes as much as 12 inches across, with a correspondingly large fruit. It begins life as an epiphyte on a Palm

or other tree, and, eventually killing its host, descends to the ground and forms a large widely-spreading shrub or a tree, according to its position.

The fruit is conical in shape, about 6 inches long and 3 inches through at the base, of a leaden-grey colour, and much too large to be carried off by a bat or bird, which alone could deposit the seeds on the branch or in the fork of a tree, a condition requisite for its growth.

F. zeylanica, an allied species, has moderately large flowers and globose fruits of the same grey colour, 1½ to 2 inches in diameter, which are apparently disseminated by civet-cats. It does not appear to be epiphytic, and most of the other species of the genus have small fruits which can be carried off by birds or by civets, and the seeds disseminated on rocks, or, when epiphytic, on trees, by these animals. But *F. auriculata* cannot be disseminated in this way, so it has adopted another method. When ripe, the conic fruit splits at the apex into 4 or 5 rather irregular segments, which recurve and spread out, so as to expose the innumerable minute seeds lying embedded in a sweet orange-coloured pulp. This is attractive to birds, chiefly to the common Bulbul (*Otocompsa analis*), which, settling on the fruit, swallows the pulp and seeds together, later evacuating the seeds on trees in the neighbourhood, where the plant grows. In the Botanic Gardens, Singapore, the seeds swallowed by the birds were deposited on the stem of a Palm (*Livistona*) about 30 yards distant, and a number of seedlings grew up there.

Here we have a distinct transformation of a berry, too large for dissemination by birds in a normal way, modified into a dehiscent capsule, so as to obviate the difficulty of dispersal by birds. In the genus which is Indo-Malayan and Polynesian we have a whole series, from the big-fruited *F. auriculata* to the small-fruited *F. ligustrina* with fruits only ⅓ inch long, all of the same inconspicuous, dull grey-green, probably dispersed by bats. Closely allied to these, however, and formerly placed in the same genus, are the fine big trees of *Cyrtophyllum*, which produce abundance of small berries the size of a pea, of a yellow or bright red colour, destined for and popular with birds and bats.

Another good example of the modification of an indehiscent berry into a dehiscent one, or practically a capsule, is to be found in the common *Momordica charantia* (*Cucurbitaceae*). In the other species of this genus the fruit is long or rounded, and contains numerous seeds in a white pulp, chiefly formed of the placentas and pericarp. In some species there is a distinct red aril. These fruits do not dehisce, but are dispersed, apparently, by being torn to pieces by birds and mammals, who devour the pulpy placentas and, in so doing, swallow the seeds accidentally. *M. charantia* has an elongate pumpkin about 3 inches long and 1 inch or more through (cultivated forms attain a greater size). The pericarp is orange-yellow, and covered with long and short warty elevations. When ripe, it splits into 3 recurved lobes, on the inner face of which are borne numerous black seeds enclosed in a bright red aril and suspended usually from a rather large funicle. The aril is soft and sweet, but the pericarp is bitter and rather unpleasant. Here is a fruit which from a true berry is transformed into a capsule by the mere splitting of the pericarp, which becomes much swollen in fruiting, very much in the same way as the *Fagraea*. The fruit is too large to be carried off by any but large birds, but by the aid of the bright-coloured aril, and dehiscence, it is well adapted for dispersal by small birds.

A somewhat similar style of modification, for purposes of bird attraction, is the dehiscence of the spike of fruits of *Carludovica palmata*, the Panama-hat Palm (*Cyclanthaceae*). This South American plant is stemless, and produces, from among the tuft of leaves, an elongate green spike of fruits, about 6 inches long and 2 inches through, resembling that of an Aroid, pendulous on a peduncle about 1 foot long. When ripe, the inconspicuous green spike splits

at the tip and eventually to the base along one side (the upper one), and is reflected into the form of an oblong plate, bearing the numerous orange-scarlet drupes. Not only is the whole inner face of this a brilliant colour, but the rachis of the spike from which it is detached is also scarlet-orange. The whole thus expanded spike is therefore very showy, and must be extremely conspicuous in the dark shadows of the Brazilian forests, and would attract the attention of any ground birds or of others flying low in the woods.

Dry Dehiscent Fruits becoming Baccate.—The modifications by which a berry may be evolved out of a dry dehiscent fruit capsule or cone is also quite simple. It practically amounts to the ripening of the seed before the dessication of the walls of the pericarp, or, in the case of a cone, before the drying up of the scales. In *Dianella* the young fruit in section shows the 3 cells of the ovary unfilled by the swelling of the pericarp and placentas, and the ovules separated from the opposite walls by a space, exactly as they are in the rest of the *Anthericeae*, which all have dry, dehiscent capsules. Then the walls of the pericarp retain their succulence and thicken, so that the fruit becomes a berry. In most of the species the berry is blue, light or dark, white inside, but sometimes all white (I observed in Singapore that plants with blue flowers had blue fruit, and those with greenish-white flowers white fruit). The allied Malayan genus, *Rhuacophila*, has a black fruit. *Dianella* is a genus of herbs (*Liliaceae*) which is far more widely spread and common than any of the section to which it belongs. The headquarters of the genus is Australia, where are a number of species, whence it has radiated to many islands, Polynesia, Fiji, Tonga, Cook, Rurutu and Hawaii, to the Malay Islands, India, Ceylon, Malay Peninsula, Madagascar and all the Mascarene Islands to Hainan, China, Liukiu Islands and Formosa. There can be little doubt that these widely-distributed plants owe their success to the conversion of the capsular fruit into a conspicuous berry, allowing of their dispersal by birds.

The South American *Xiphidium*, usually referred to *Haemodoraceae*, has a very similar fruit, at first appearing to be capsular and then being converted into a scarlet or orange-coloured berry. It is a herb of the style of *Dianella*, and is widely spread over the West Indies and South America, inhabiting forests.

The Junipers still retain in their baccate fruit traces of the original scales which, like the Cypresses, they formerly possessed. The transformation of the cone, opening to let fall the seeds, to a small berry made conspicuous and beloved of birds, has been the cause of the very wide distribution and abundance of this genus in both hemispheres. A young *Callitris* cone is berry-like, and closely resembles the fruit of a Juniper, though it is larger. When the seed is ripe, the dry scales separate and release the winged seeds. In the Juniper the scales remain connate, only their tips being visible. The cone has become a berry, the seeds are not winged, and ripen in the closed scales, which never separate. The fruit is reduced in size so as to be easily swallowed by the smaller birds, and is covered with a whitish bloom which makes it conspicuous against the foliage. The older *Callitris* is now very restricted in area, while the later evolved Juniper, thanks to its baccate fruit, is the most abundant shrub in the north temperate region.

The transformation of the little capsule in *Hedyotis congesta* and of the nucules of *Gomphostemma* into small, white, pulpy bird-disseminated fruits, and the change of the capsular fruit of *Hypericum androsaemum* into a black berry in New Zealand, somewhat similar modifications to the above-mentioned ones, have already been described.

Another modification of the fruit, by which capsular fruits are made attractive to birds and by them dispersed, is effected by the persistence of the sepals, and sometimes the petals, which enclose the capsules and become fleshy and coloured. This occurs in some of the *Dillenias*, as in *D. meliosmaefolia*.

In this the sepals, at first comparatively thin and dry, in fruiting, close over the ovaries and become yellow, fleshy and sweet, quite eatable, though somewhat acid, forming a ball-like fruit 1½ inches through.

Gaultheria (*Ericaceae*), a genus of mountain shrubs, is another instance in which this sometimes occurs. In *G. oppositifolia* and *G. fagifolia* the calyx remains unaltered, merely drying up, the fruits remaining as dry capsules. In *G. rupestris* and *G. perplexa* the calyx appears to be sometimes swollen and fleshy in fruit, and attractive to birds, and sometimes remains dry and withered. In *G. antipoda* the calyx is always fleshy and enlarged in fruit, and purple or red, and the fruits are naturally bird-dispersed. The genus is widely dispersed on mountain ranges. *G. fragrantissima* is found in India, China, the Malay Peninsula and Sumatra, *G. nummularioides* in China, India, Java, Sumatra, *G. borneensis* in China, the Philippines and Borneo. The fruits of these widely-spread plants are fleshy, white, red or blue, to black. The genus is widely diffused in America. In *Coriaria* (*Coriariaceae*) it is the petals which persist, and, closing over the 5 to 8 cocci of the ovary, become fleshy and transform the capsular fruit into a berry, in some cases purple-black, in others, *C. japonica*, red, and *C. terminalis*, orange. These brightly-coloured fruits are very popular with birds. They range from South America and New Zealand to temperate Asia and South Europe.

THE ARIL

A paper by Planchon (*Ann .Nat. Sc.*, ser. iii, vol. 3, p. 11, with plates xi and xii) gives an account of the formation and forms of the adjunct to the seed, known as the aril. He distinguishes between true and false arils, or arillodes. The aril in the Passion-flowers (*Passiflora*) forms, after fertilisation, as an expansion of the end of the placenta, which eventually covers the seed and is open at the tip. This form he classes as a true aril. In *Euonymus* the aril is a false aril or arillode. It is formed by a dilatation of the edge of the exostome of the ovule reflected over the opening. In *Ravenala* the aril consists of a number of coloured hairs growing from the funicle round the hilum, sometimes joined into finger-like processes, and blue in *R. madagascariensis*, and sometimes woolly and red in *R. guyanensis*. It is not always possible, at present, to allocate these forms of aril to their correct groups, as of so many fruits possessing arils (in the wide sense) the evolution of the seed is unknown, nor even can one be sure whether the fleshy pulp surrounding a seed is an aril or a softened part of the testa. Thus the pulpy portion of the seed of *Lansium domesticum*, the Duku (*Meliaceae*), is probably an aril, as nearly all the *Meliaceae* have more or less traces of one.

The actual origin of the aril, however, has comparatively little importance in the questions of dispersal of seeds, though the matter is a point of some interest in the evolution of species.

Arils or arillodes are found in many orders, especially those with capsular fruits, chiefly *Celastrineae*, *Euphorbiaceae*, *Meliaceae*, *Myrtaceae*, *Connaraceae*, *Zingiberaceae* and *Marantaceae*. The caruncle (*Elaiosome*), or oil-body attractive to ants, is of the same nature, and is described under Dispersal by Insects (*see* p. 519).

It would indeed be difficult for the seeds of many large capsular fruits to be dispersed at all except for the presence of the aril. Capsular plants, especially trees, shrubs or climbers, would often have little chance of dispersal in the forest, or in places where the vegetation is dense, without some such means. The seeds would merely fall to the ground in a mass at the foot of the tree, and would not be carried away either by wind or water, but, germinating at the foot of the tree, would perish.

The aril or arillode may only remain at the base of the seed, or it may partially or entirely cover it. It must be firmly attached to the seed, if it is only basal, for

bird-dispersal, otherwise the bird might merely eat it off and leave the seed. It is essential that the bird should carry away the seed with the aril.

In most cases the aril is brightly coloured and of a different colour to the capsule if it covers the seed, or to the rest of the seed if it is only partially covered. The commonest colours are orange, yellow or red; white arils, contrasting with an orange or red capsule, occur in *Scitamineae*, *Adenia* (*Passifloraceae*), and some other fruits. Blue arils are very scarce, the only one I know being that of *Ravenala madagascariensis* (*Musaceae*).

In some cases the capsule is green and the aril red (*Microtropis*, *Glyptopetalum*), or dark brown with red or orange aril (*Baccaurea* spp.). In many the capsule is orange and the aril red (*Casearia*, *Ervatamia*), or the capsule pink, the aril orange (*Euonymus*), or the capsule white, the aril red (*Dysoxylon angustifolium*), or the capsule red or orange, the aril white (*Adenia*, *Alpinia*).

Where the aril completely covers the seed, it is usual for the seed-testa to be fawn colour or whitish, as in many wild nutmegs, but where it only partially covers it, the testa is usually black, forming a fine contrast with the brightly-coloured aril and capsule. A good example of this is *Dysoxylon cauliflorum*, where the capsule is orange and splits into 4 lobes, showing the shiny black seed with its scarlet aril (Pl. XVI, figs. 3 and 4), and *Momordica charantia*, where the widely-spreading lobes of the fruit are orange-coloured, the aril crimson-scarlet and testa of the seed black, and the beautiful scandent shrub *Connarus ferrugineus*, with large crimson pods containing a black seed half covered with a yellow aril.

In plants of the temperate regions the fall of the leaves on the approach of winter, before the fruit is ripe, as in *Euonymus europaeus* and *Celastrus scandens*, leaves the bush very conspicuous from the abundance of gay-coloured capsules and arils. Where there is no special fruiting season, in tropical regions, the bright capsules, with their showy arils just peeping out between the edges of the valves, attract the notice of wandering birds as they fly through the forest.

Yew.—Among the *Gymnosperms* the only plant now existing which possesses a true aril is the Yew tree (*Taxus baccata*). The pink, sweet, glutinous cup which surrounds the seed is an outgrowth from the base of the ovule, and so is a true aril. The seed is of a dull green colour, and is believed to be more or less poisonous. The Yew fruit is very popular with birds, especially of the thrushes, who usually swallow it, seed and all, and regurgitate the seed, though they swallow and also pass the seeds at times. It is owing to these birds that the Yew tree is so widely distributed. It is found all over Europe, in Algiers and Northern Persia, India, Burma, Siberia, China and Japan, the Philippines and Celebes, and is reported from one spot in Sumatra. In America it is found abundantly from Canada to Mexico. It was formerly very abundant in the Azores, but has been nearly exterminated. According to Ogilvie Grant, the missel-thrushes, which are the great dispersers of this plant, are very rare stragglers to the Azores (Guppy, in "Plants, Seeds and Currents," p. 437). The Yew appears to be quite absent from Africa, except Algeria, and from Southern India, Australia and Polynesia, as well as South America. There is only one species of the genus existing, though it varies to some extent, as might be expected, and several species have been made of it. The earliest record of it is in the Miocene period.

Among the *Monocotyledons* arils are comparatively scarce, and chiefly occur in the *Zingiberaceae* and *Marantaceae*. In the *Alpinias* of the *Catimbium* section, with large racemes of showy flowers, the capsules are globose, orange or red, about 1 inch through. These partly dehisce, and disclose numerous hard, black, aromatic seeds enclosed in a sweet white aril. The *Amomums* also have frequently rather large red capsules borne on short racemes close to the

ground, which partly split, and contain arillate seeds resembling those of *Alpinia*. These are probably eaten by ground-birds and rodents. The hot, peppery, aromatic seeds are not crushed by these animals. In the *Marantaceae* some of the *Phryniums* have a whitish capsule enclosing oblong brown seeds with a linear white process or aril on each side. *Phrynium malaccense* has red capsules borne halfway up the stem. *Stachyphrynium Jagoranum* has a short spike, 2 inches long, hidden among the leaves, with a small oblong capsule containing 2 brown seeds with a white aril with 2 long claws (Pl. XVI, fig. 10). *Thaumatococcus*, of tropical Africa, has a large red 3-angled capsule on a short raceme from the base of the stem, with globose seeds, and has an intensely sweet film, which is presumably an aril. Among the *Musaceae*, *Ravenala madagascariensis*, the Traveller's Tree, has capsules in the form of large woody boats containing hard black seeds in an oily blue aril, or, strictly speaking, an arillode. *Forrestia*, a jungle genus of *Commelinaceae*, has oblong pink capsules borne in the axils of the leaves, with small seeds enclosed in an orange scarlet aril, very conspicuous. These dark forest plants, the *Marantaceae* and *Forrestia*, must be fed on by the small jungle Sun-birds, *Nectarinidae* (as, indeed, in the case of the *Marantaceae* we know they are), which flit about amongst the low herbs of the forest in search of spiders and other insects, and the ground-game, pheasants and such birds, also doubtless search for these low-growing arillate fruits.

Among *Dicotyledonous* plants arils are common and very characteristic of some orders. *Wormia* is a Malay genus of *Dilleniaceae*, trees and shrubs of large size with very fine yellow or white flowers. In *W. suffruticosa* the sepals close over the 5 free carpels till they ripen, when they expand into a flower-like circle of pink open lobes, containing a number of black seeds with a fimbriate scarlet true aril rising from the base. The carpels open out in the early morning, and are as conspicuous as flowers, but in an hour or so the seeds are carried off by bulbuls and other birds, so that it is often difficult to find a single seed left on the bush by 9 o'clock. *W. tomentella*, a tree, has the expanded carpels a dull white, hardly as conspicuous as those of *W. suffruticosa*, and is a much more local plant (Pl. XVI, figs. 1 and 2).

The closely-allied genus *Dillenia* differs from *Wormia* in the fact that the sepals, after closing over the carpels, do not open again, but increase in thickness and fleshiness. The sporadic but widely-scattered *D. indica* has very large fruits, often 6 inches through the closed sepals, and is dispersed by rivers. The others, e.g., *D. meliosmaefolia*, etc., have smaller, round, fleshy, yellow fruits, sweet to taste, and are dispersed probably by bats or rodents. In *D. Scortechinii*, with green fruits, the ground beneath the tree is often strewed with the fallen fruits, practically wasted, a great contrast to the empty carpels of the *Wormias*.

Adenia (*Modecca*) (*Passifloraceae*) is a genus of climbers widely distributed, in which the fruit is a globose or conic capsule of a bright red, which hangs down from the branches and dehisces into lobes, from which hang a number of grey or black seeds in white cups on the end of long white fleshy funicles. These white cups, enclosing half or more of the seed, are true arils formed of a dilation of the upper end of the funicle (Pl. XVI, fig. 9). These climbers are usually to be found in conspicuous spots on the edges of forests or in open thickets. The funicle and aril are considered by the Malays to be poisonous, but they are eaten by birds. Species occur in Africa and Madagascar, India and Andamans and Nicobar Islands, Yunnan, the Malay Peninsula and islands, to the Philippines and Australia. The whole order is scarce in tropical Asia, and as Africa is rich in capsular species of *Passifloraceae*, and *Adenia* is abundant there, I think it is quite clear that this genus has originated in Africa, and been conveyed by birds to and through Asia eastwards.

Acacia cyclops, of Australia, is another example of the aril being formed of the long funicle. The pods split on the tree, and disclose 4 or 5 flat black seeds surrounded by a fleshy red aril consisting of the funicle. The contrast of the shiny black seed in the red fleshy circle is very marked. *A. melanoxylon* has a very similar flesh-coloured aril formed of the funicle, which lies round the edge of the seed, being twice bent on itself (Hildebrand, *Ber. Deutsch. Bot. Ges. Bd.*, i, 1883, p. 461) and *A. homalophylla* has a similar one.

Polygala.—The ordinary Milkworts (*Polygala*), open-country plants and mostly small herbs, have the seeds furnished with a small caruncle or elaiosome (an oily growth on the end of the funicle) destined to attract ants, which carry these small seeds to or towards the nest, to feed on the caruncle. (*See under* Dispersal by Insects, p. 520.) But in some jungle species this caruncle develops into an aril. *Polygala venenosa* and *P. pulchra* are shrubby species inhabiting dense Malay jungles. The flowers are in axillary racemes, and are succeeded by capsules, 2-lobed and rounded, about ⅓ inch across, purple, and containing 1 or 2 seeds enclosed in a scarlet aril. These shrubs are about 2 or 3 feet tall, with large and broad leaves, adapted altogether for forest life. *P. arillata*, of South India, is somewhat similar, and has a red aril covering three-quarters of a black seed.

Euonymus europaeus (*Celastrineae*), the Spindlewood, is, when in fruit in the autumn, one of the most conspicuous of shrubs in England, and is well known to most people. The pendent capsules are bright rose colour, and the seeds, which hang from the placentas, are covered with a sweet orange aril, or, more correctly, arillode. As the leaves fall before or as the fruit ripens, a bush in fruit and bare of leaves is very conspicuous, and a great attraction to birds, especially thrushes and blackbirds, which pluck off and swallow the pendent seeds, and thus readily disseminate them. In this species, as in most others, the seed beneath the aril is of a brownish-white colour. In *E. verrucosus* the aril does not completely cover the seed, but surrounds it in the form of a cup, somewhat similar in appearance to the cupular aril of the Yew. In this fruit, as the aril only touches the seed at the bottom, the seed is shining black, forming an additional contrast in colour. The genus is a very widely distributed one, occurring not only all over temperate regions, but in the tropics also. Species are found in Europe, temperate and tropical Asia, Australia and North America as far south as Mexico. In *E. oxyphylla* the seeds in their bright orange aril hang from the tip of the capsule valves, and are very conspicuous, so that the birds clear them off as quickly as they ripen (Pl. XVI, fig. 7).

Celastrus is a genus of scandent shrubs or erect bushes with rather small round capsules, generally yellow, with small seeds enclosed in a showy red arillode. Absent from Europe, it occurs in the Algerian Sahara, India, Malay Peninsula and islands, China and Japan, Australia, Polynesia, Madagascar and Aldabra and North America to Mexico. *C. paniculatus*, with panicles of fruits, is found in China, India, the Malay Peninsula, Christmas Island, the Philippines and New Caledonia. The arillate seeds do not hang out from the globose capsules, as in *Euonymus*, but the capsule opens widely and exposes the red arillate seed lying in the orange yellow valves, very conspicuous, and the seeds, being small, are greedily sought by small birds. This probably accounts for the very wide distribution of the genus.

Another form of showing the arillate seed is obtained by the capsule splitting longwise on one side, and exposing the seed with bright red or yellow aril lying in the capsule. Such a form is common to the *Connaraceae*. Usually in these the pod or follicle is pink or red, the aril yellow, half covering the black seed, but some *Connarus* have the pod yellow and the aril red, the seed being black. In *Agelaea Wallichi* the pod is red and the aril red. In these the aril

only covers part of the seed, so that in most we have three contrasting colours. The seeds are generally solitary, rarely 2 in a pod.

In the shrubs or small trees of *Casearia* (*Samydaceae*) there are numerous angular seeds in the yellow capsule covered with a red aril. The flowers are few and axillary, so that the fruits, though conspicuous when ripe, are few and scattered.

Baccaurea (*Euphorbiaceae*) are Malayan trees with rather varied fruit. Two or three species (*B. parviflora*) are small trees in which the female flowers are in very numerous racemes at the foot of the stem. The fruiting racemes actually touch the ground. These have fleshy fusiform berries of a deep claret colour, and are doubtless dispersed by rats and such terrestrial mammals. But most species have the fruits borne on the branches, capsules yellow or brown, dehiscing into 3 valves, or irregularly, and exposing seeds entirely covered with a yellow or orange aril. In *B. minor*, and some others, when the fruit dehisces, the dark yellow valves fall off, leaving the seeds, with their juicy yellow arils hanging on the placentas, very conspicuous. In the Tampoi (*B. malayana*) and the Rambeh (*B. Motleyana*), both popular fruits, the seed is enclosed in a sweet white pulp. The fruit of the latter is indehiscent. I suspect that this pulp is arillate, in part, at least, but it may be a modification of the testa. These fruits are dispersed by fruit-bats or squirrels.

The Nutmegs (*Myristicaceae*) are trees of moderate to large size, distributed from South India through the Malay regions, where they are abundant, Australia, Polynesia and South America, Africa and Madagascar. The fruit is a 1-seeded capsule, the seed of which is wholly or partly covered with a yellow, or rarely crimson, lacerate aril. In the Nutmeg of commerce (*Myristica moschata*) the fruit is fleshy, yellowish-white and globose, or pear-shaped. When ripe, it splits part way from the top into 2 thick valves, and exposes the seed, enclosed in a dark brown shining testa and covered outside by a beautiful crimson aromatic aril, the mace, which dries yellow or orange (Pl. XVI, figs. 5 and 6). This is almost the only aromatic nutmeg, only a few having any trace of aroma in the aril or seed. The other species have fruits varying from $1\frac{1}{4}$ to 3 inches long, and often yellow or orange, frequently woolly. The arils, of a yellow or orange colour, cover the base only, or more or less completely the whole seed, which is usually oblong. These trees are most closely associated with the great Fruit Pigeons, *Carpophaga* and *Myristicivora*, which, assisted by hornbills—and in Ceram and New Guinea by cassowaries—disseminate the plants far and wide.

There are several genera made out of the old genus *Myristica*, but they are separated from floral differences, the form of the fruit being much the same in all. The larger fruits have oblong cylindric seeds, which would probably be more easily swallowed by large birds; the smaller ones are sometimes globose, and eaten by small birds.

Waxy Arils.—The *Sindoras* are big or vast trees (*Leguminosae*), natives of the Malay Peninsula and islands, with round, flat, thin 1-seeded pods, and (except for one species) armed with scattered prickles on the outside. The pods dehisce either on the tree or after they have fallen, and disclose a thin, round, flat seed, at the base of which is a broad, flat, yellow waxy portion, nearly as large as the seed, but not overlapping it, as an ordinary aril does. King describes it as an "arillate funicle," and, indeed, it seems to be a modification of the funicle, and not an outgrowth of the ovule base, as in a true aril. This is not juicy, as in ordinary arils, but waxy. It is nibbled away by mice or other rodents, after the fruit has fallen to the ground and dehisced. (Pl. XVI, fig. 8).

A somewhat similar wax aril occurs in the woody Durian, *Neesia* (*Malvaceae*). This is a tall tree of the forests of the Malay Peninsula, with a large wooden

fruit like a durian, of a blue-grey colour. It only dehisces halfway, and discloses on the inside of the valves a quantity of irritating hairs and some small mahogany-brown seeds, with a yellow wax aril at the base. The whole fruit, after dehiscing, falls to the ground, still containing the seeds, though some are thrown out by the fall (Pl. XVI, fig. 6). The yellow waxy aril, very similar to that of *Sindora*, though very much smaller (red, according to Beccari, in *N. pilulifera*) is eaten by some small rodent, and possibly also the waxy aril is eaten by ants, the seed being not too big for them to carry off.

In the case of *Sindora* I have distinctly seen marks of rodent incisor teeth on the aril, and in *Neesia* the aril was also nibbled by some animal. Of course, as the mice and rats only come out at night, it is not possible to see them eating these arils.

Beccari (" Malesia," iii) calls the outgrowths round the seeds of *Durio*, etc., " arillodes," and says they are an outgrowth of the funicle. In most species of *Durio* the aril is soft, creamy, and white, and completely covers the seed. In *D. pinangianus*, with pink flowers, the arillode is also rose colour. In *D. testitudinarum* Becc. the arillode does not quite cover the seed, and in *D. oblongus* it only covers two-thirds of it. *D. testitudinarum*, a Borneo species, bears the fruit at the base of the tree, and it is said by Beccari to be eaten by tortoises. The pink-arilled *D. pinangianus* is called in Malay Durian Burong (Bird's Durian), and perhaps the pink colour makes it attractive to birds.

Boschia is a genus of a few small trees in the Malay Peninsula and neighbouring islands. The fruit is $1\frac{1}{4}$ inches long, spiny, and of a brilliant scarlet. The seeds, black, and nearly 1 inch long, have a yellow arillode, cup-shaped, lobed and waxy, about half its length. It is altogether a very beautiful and conspicuous fruit, and is doubtless dispersed by birds.

In the *Leguminosae* there is another genus in which the seeds possess a waxy aril, *Afzelia*, but the occurrence of this aril is confined to some African species only. *A. cuanzensis* has a large woody pod about 6 inches or more in length, containing a number of black seeds, with a waxy-red cup-like aril at the base. In *A. africana* the aril is similar but yellow. Specimens of picked-up seed of *A. cuanzensis*, brought from Tanganyika territory, show distinctly the toothmarks of some small rodent along the upper edge of the cup, and in some seeds of *A. africana* in Kew Herbarium the aril seems to have been nibbled by some animal. The aril is firmly attached to the base of the seed, and is not readily detached, so that a rodent gnawing the aril would probably take the seed along with it. In the Asiatic species of the genus the seed is not arillate, and is much larger and flatter, and is dispersed by water.

In a number of seeds the outer coats of the testa are sweet and more or less pulpy, and form an attraction to birds. The fruits are always capsular, that is to say, they split so as to show the pulpy coloured coating, though sometimes they are only 1-seeded. In many of these fruits the life-history is so little known that it is difficult to say if the eatable portion is an aril or arillode, or the modified testa of the seed. It is quite clear, I think, that the azure-blue coat of the seed of *Peliosanthes* is merely modified testa, and the outer black coat of the seed of *Sterculia* is clearly testa only, but in other fruits I am not at all sure as to the real origin of the part which attracts and is eaten by birds.

I give herewith some account of the more interesting fruits of this nature :—

Sterculia (*Sterculiaceae*) is a large and widely-spread genus of trees or shrubs from about 4 to 80 feet tall. The fruit consists of 5 carpels (or occasionally fewer by abortion), which develop in the follicles from 4 to 6 inches long, and split septicidally, forming lanceolate, or ovate lanceolate lobes of a magnificent and brilliant scarlet colour, or occasionally of a rosy red. From the lower edge of the opened carpels hang 4 or 5 blue-black oblong seeds, forming a

striking contrast with the bright scarlet of the carpel. Beneath the thin black outer layer of the seed is a very thin, white, pulpy layer, overlying the hard inner coat of the seed (Pl. XV, fig. 4). Though this thin white layer is all there is for a bird to eat on the large seed, these seeds are extremely popular with birds. A tree of *Sterculia Jackiana*, about 8 feet tall, grew close to my house in Singapore, and as soon as the carpels dehisced in the early morning, the seeds were carried off by some bird. I could never see a bird carry one off, but, in spite of the size of the seed, it must have been one of the small birds, as no pigeons, except *Turtur*, certainly ever came so near the house. Guppy seems rather puzzled with the distribution of this genus, as he could not conceive that seeds with so little to eat on them were attractive to birds, yet the trees are found in the Polynesian Islands, Fiji, New Hebrides, and New Caledonia, though not in Tahiti or Hawaii. He points out that the seeds do not float, and though the unopened follicles, and, indeed, the opened follicles, are constituents of sea-drift, the ripe fruits dehisce on the tree. I have no doubt that the seeds are swallowed in these cases by pigeons and so conveyed to the islands. The genus is found in Africa, Asia, and South America, and is reported to occur in the Eocene beds of Europe. The interest in it lies in the very small amount of food that a bird can obtain from so large a seed, and we may compare it with the very small arils on the small seeds of the showy follicles of *Wormia*, which, as I have mentioned, are extremely popular with birds. Though in the neighbourhood of the trees of *Sterculia* and bushes of *Wormia* were abundance of trees of Figs, *Cyrtophyllum*, with orange berries, and *Rhodamnia*, with black berries, all popular with bulbuls and such birds, the brilliantly-coloured *Sterculia* and *Wormia* were the first attraction, though they had much less nutriment to offer.

A curious, and I believe unique, form of fruit is that of *Erythropalum scandens* (*Olacineae*). It is an oblong drupe of a rather dull but conspicuous red. When ripe, the red pericarp splits into 4 or 5 linear lobes which recurve, and in the centre stands an oblong, blunt, dark blue seed, which is presumably swallowed by a bird. The plant is a slender climber on Malay forest edges.

Another group of trees with coloured seeds which apparently afford very little nutriment to birds, but which undoubtedly are disseminated by them, is the genus *Glochidion* (*Euphorbiaceae*). The trees are about 2 or 3 feet tall, and bushy, bearing a large number of brown many-seeded capsules about $\frac{1}{4}$ inch across. When ripe, these capsules dehisce, the valves fall off, leaving a circle of usually 6 hemispheric seeds, covered with a very thin orange or pink covering. It is possible that this is a true aril, for many allied genera possess a fleshy conspicuously-coloured orange or red covering to the seed which is certainly arillate. *Baccaurea latifolia*, for instance, has a brown, woody, globose capsule, of which the valves fall off and expose a seed covered with a fleshy orange aril.

The *Glochidions*, *G. leiostylum*, *G. desmocarpum*, *G. sericeum*, which have these exposed pink or orange seeds, grow in open spots, and are not uncommon in secondary woods. The seeds are very popular with small birds.

Iris foetidissima.—In this well-known English plant the pale green capsules open in autumn into 3 valves, each bearing 2 rows of red fleshy seeds, very conspicuous. The pulp of this is apparently not arillate, but a part of the testa. In most of the other species this outer coat is not eatable and is inconspicuously coloured. In *I. pseudacorus* and *I. sibirica*, riparian plants, the outer coat is reddish-brown, not detachable when the capsule dehisces, and serves as a float to drift the seeds away. In *I. foetidissima*, a woodland plant, this outer layer has become pulpy and conspicuously red, so that the plant can be, and is, dispersed by birds.

In the *Gymnosperms* we have cases where the thin testa is coloured and

attractive to birds. The seeds of *Gnetum* are often pink or yellow, oblong, ¼ inch long, and borne on spikes. They have been found in the stomachs of pigeons. The plants are Indo-Malayan climbers, or rarely bushes or trees. In the *Cycadeae* the outer layer of the testa is often somewhat pulpy and orange coloured, and the seed is sometimes quite small enough to be swallowed by a bird. Marloth says that those of *Encephalartos Altensteinii*, of South Africa, are carried off by birds and rodents.

The *Pithecolobiums* are trees of no very great size, belonging to the order *Leguminosae*, which usually have curiously curled pods of a dull or bright red, and black seeds, apparently always quite hard, and having no eatable portion. *P. ellipticum* has a pod from 3 to 7 inches long, twisted into a circle or spiral, and 1¼ inches wide, and of a dull red. The seeds hang down from the placentas and are oblong rounded, ¾ inch long and over ½ inch through, black, with a pale bluish bloom. It is a common and rather widely-spread tree all over the Malay Peninsula, Java and Sumatra. In *P. clypearia* the pod is smaller, 4 or 5 inches long, orange outside and red inside, the seeds black. Most of these trees, and notably *P. microcarpum*, are very showy in fruit, the orange pods being very conspicuous. The seeds disappear very soon, and are evidently taken by birds, though there seems no reason why they should eat them, as, unless they crush them, there seems to be no nutriment in them.

Imitation Arils.—The seeds, with very thin coloured testa, which, though containing so little nutriment in proportion to the bulk of seed swallowed, are popular with birds, lead up to a class of seeds which has always been puzzling. They are brightly coloured red and very conspicuous, but are hard and stony all through, and do not even carry the thin, soft outer coat of *Sterculia* or *Glochidion* seed. As the only nutriment they could produce (the internal cotyledons) cannot be utilised by a bird without breaking up the seed and destroying its germinating power, it is difficult to see of what advantage the red colouring can be to the plant.

The trees all belong to the order *Leguminosae*, and include *Abrus precatorius*, *Adenanthera bicolor* and *A. pavonina*, and several species of *Erythrina* and *Ormosia*. In *Abrus* and *Adenanthera bicolor* the very hard seeds are half black and half scarlet, giving the appearance of a black seed with a scarlet aril half covering it. In *Adenanthera pavonina*, and some of the *Erythrinas*, the whole seed is red and shining.

Adenanthera pavonina is a fairly large tree, the pods of which dehisce before falling, exposing the brilliant seeds, contrasting with the black outside of the valves. Guppy ("Solomon Islands," p. 293) records finding cracked seeds of it in the gizzard of a Nicobar Pigeon (*Caloenas nicobarica*), and in "More Letters of Charles Darwin," ii, 349, is quoted a letter from Fritz Muller, saying :—"I wrote to India on the subject, and I hear from Mr. J. Scott that "parrots are eager for the seeds, and, wonderful as the fact is, can split them "open with their beaks. They first collect a large number in their beaks, and "then settle themselves to split them, and, in so doing, drop many. Thus "I have no doubt that they are disseminated." The tree is largely distributed by man, being used as a shade tree, and the seeds often carried about by children and natives for necklaces, counters, etc. I have little doubt that birds do disperse them to some extent, possibly being attracted by the colour. They may swallow them to act as stones in the gizzard (as frigate birds do with *Guilandina*). *A. bicolor*, of Ceylon and the Malay Peninsula, has its 2 coloured seeds hanging out of the pod on the funicle when ripe, and are even more conspicuous. A bird flying past the tree might carry one off, thinking it was a black seed with a red aril, and, not finding it eatable, drop it at some distance. This tree, occurring more sporadically and in forests, is almost certainly bird-dispersed.

Erythrinas are trees of some size, in which the seeds, 1 or more in a pod, are brilliant red, in many species at least, and quite hard. Most of these trees are sea-dispersed and very characteristic of oceanic islands. Layard ("Ibis," vi, 1882) records that in New Caledonia a small crow and several species of parrot feed on the seeds of *Erythrina*, and Alan Cunningham mentions in his Diary that he found an *Erythrina* in the Dividing Range, Australia (evidently *E. vespertilio*), and writes :—" Its last year's pods continued hanging on the extremities " of the branches, and although pigeons, which abound in these woods, and " other birds had eaten most of these seeds, still, many of them, a brilliant red " colour, were found among grass beneath each tree."

Even if the birds dò eat and crush these hard seeds, some may pass through the bird insufficiently injured to prevent germination, as happens in the case of the grains eaten by granivorous birds at times, but a great deal more evidence is required on this subject.

PART III

COMPOUND FRUITS.

WHEN the small, usually pulpy, fruits of different flowers are crowded into one head, so as to form a dense mass, the whole body is called a "compound fruit." It is the natural result of a short spike, or capitulum of fruits with pulpy pericarps. If the separate fruits are dry, they are, in such cases of agglomeration, capsular, and the seeds merely fall out, or are winged and light, and so wind-dispersed. Occasionally the bracts surrounding the head are wing-formed, and in this case the flowers may be all abortive but one (*Sphenodesma*), and the 1-seeded head wind-dispersed.

In *Nauclea* (*Rubiaceae*) the small flowers are usually sessile in rounded heads. In *Uncaria*, which may be taken as a primitive form, the ovaries are quite separate, and in many species stalked. The fruits are elongate capsules with winged seeds, wind-dispersed. In *Mitragyne* the flower-head is more compact, the flowers sessile. The capsule dehisces at the top and emits the light-winged seeds, and the same is the case in *Adina* and *Nauclea*. In *Anthocephalus* and *Sarcocephalus*, trees of open country of Indo-Malaya, in *Breonia*, of Madagascar, and *Cephalanthus*, the Button-bush of America and Africa, the whole head of fruits is agglutinated into a mass, and they are pulpy and do not dehisce, nor are the seeds winged. The heads of fruits are pulpy and firm, dull brown in some species, but red in the Negro-head Peach (*Sarcocephalus esculentus*) and some others. *Cephalanthus occidentalis*, the Button-bush of America, appears constantly in the list of bird foods in North America. I believe, however, that most of the brown-fruited inconspicuous species in the Malay Peninsula supply food to fruit-bats. They are all trees of forest edges and open spaces.

Morinda is another Rubiaceous genus in which a large number of fruits are condensed into one mass, often large and juicy. The compound fruit of *M. umbellata* is of a very conspicuous orange colour when ripe, and ½ inch through. It is a common scrambling shrub in open country, sandy heaths, and sea-coasts, ranging from India, through the Malay region, to China and Australia.

M. Ridleyi, a forest climber, has conspicuous black heads. It is found in the Malay Peninsula. *M. elliptica* is a very common small tree which comes up abundantly in Lalang wastes (grass fields of *Imperata cylindrica*). The fruit-head, ½ inch through, is always green and inconspicuous. I believe it is dispersed by the small fruit-bats. I have never seen birds eat it.

M. citrifolia has a large, pulpy, white translucent fruit-head 3 inches long and 2 inches wide. It chiefly occurs in cultivated ground, and the fruit is eaten (though unpalatable) by natives. The very small seeds are scattered through the pulpy mass. It is too big for birds to carry off, but they might bite bits containing seeds out of it. I think on land it is dispersed by mammals and human beings. The seeds are adapted for sea-dispersal (*see* pp. 295, 370). One of the South American *Compositae*, *Wulfia stenoglossa*, has the achenes swollen and juicy, black and sweet, the whole head much resembling an English blackberry. This, introduced into the Botanic Gardens, Singapore, proved very attractive

to the bulbuls, which ate the fruit and disseminated it all round under the bushes and the trees for some distance. *Cornus capitata* (*Benthamia fragifera*) is a Himalayan bush or tree with very closely-allied species in China and Japan. The fruits are connate into a round, bright red head (nearly as large as a nectarine), which is eaten by natives and children, and doubtless also by birds. Allied to this plant are *Cornus Nuttalli*, of Western North America, and C. *florida*, but in these the bright carmine fruits are separate, though in a compact head, and are eaten by pigeons. In all these dense-headed *Corni* the head of small flowers is surrounded with large white bracts to set off the inconspicuous flowers. Before ripening, however, these bracts wither and fall off. In the other species of the genus the flowers, larger and more conspicuous, are in spreading corymbs.

Among the *Urticaceae* we have a number of compound fruits. The small achenes are often borne in heads or dense spikes, and the ovaries in fruit become fleshy or juicy, and form a sweet pulpy fruit. In the genus *Ficus*, dealt with separately, the eatable portion is the fleshy receptacle.

The largest of these compound fruits are those of the genus *Artocarpus*, the Jackfruits and Breadfruits. These compound fruits are large, or very large, oblong or round, either green, white, brown or yellow, and very popular with mammals, especially monkeys and civets, but also to some extent with birds. The fruits are too large to be carried off by any of these animals or birds, but are torn to pieces, and portions containing seed eaten, or the seeds scattered about. A few, *A. gomeziana*, etc., have fruits not too big for bats to carry off whole. The trees, as a rule, are tall, and the fruits borne on the high branches, but in some species grow low down on the trunk (*A. polyphemia*) and within easy reach of the wandering forest ungulates, wild cattle, pigs, elephants, etc., which doubtless feed on them, and in many cases the fruits fall to the ground when ripe, and are easily found and picked up by these animals. The allied *Treculia africana* is, according to Burtt-Davy, a popular fruit with the African elephant. *Cudrania javanica*, a scrambling spiny shrub, has the achenes enclosed in large fleshy bracts, forming, when ripe, a head of orange-coloured pulpy fruits ¾ inch through, attractive to birds and widely distributed over East Africa, India, Malaya and Australia.

Prainea scandens has a bright yellow globose head of a mass of abortive flowers and a few achenes with a fleshy perianth. It is rare, and only known from the forests of the Malay Peninsula.

Debregeasia has also small globular heads composed of achenes in a fleshy perianth, bright red and very showy. They are prickly shrubs occurring in Africa and tropical Asia. *D. squamata*, scrambling over rocks like a blackberry, with its extremely brilliant crimson-scarlet compound fruits, is very conspicuous from afar.

Villebrunea.—These are medium-sized trees of Indo-Malaya and Japan, in which the small greyish-white heads of fruit are composed of the achenes in a fleshy white perianth. Small as these fruit-heads are, they are really quite conspicuous against the dark green foliage, and very abundant on the trees, which are common in the mountain forests, and certainly much disseminated by birds. Other well-known compound fruits, much sought by birds, are the Mulberries (*Morus nigra* and *alba*). Mr. Hart-Merriam gives a long list of birds which feed on these trees in America.

Ficus.—This large genus, of about 600 species, may be taken as one of the most successful of genera. The plants are shrubs or trees, varying from 6 inches to 100 feet in height, and are distributed all over the tropics and into the warm temperate regions. The compound fruit of the Fig consists of an oblong globose or pear-shaped receptacle containing a large number of minute flowers, male, female and gall-flowers. The males are usually to be found at

the mouth of the opening into the receptacle, but often occur mixed with the females, and sometimes in separate figs. The gall-flowers are female flowers attacked by very minute hymenopterous insects (*Chalcididae*), which, entering the mouth of the fig, deposit their eggs in these flowers and, eventually hatching out, escape by the mouth, carrying with them the pollen of the males, and, entering another fig in the same way, pollinate the female flowers within. Without these minute gall-wasps the figs are unable to propagate by seed. Each species of fig appears to have its own species of gall-wasp, but there is some evidence that certain species of the latter can fertilise more than one species of fig.

There is hardly any tropical island of any size but possesses one or more species of *Ficus*, and these plants, however distant from the mainland, possess their little gall-wasps in abundance. In Fernando de Noronha was an endemic Fig, *Ficus Noronhae*. In Christmas Island *F. retusa* was abundant, and reproduced itself. Both of these, as I found, possessed abundance of gall-wasps. There is a difficulty in accounting for the presence of the fig plants on these remote islands. The very small seeds are easily transported by fruit-bats and birds, which feed greedily on the juicy receptacles, but there is a distinct difficulty in accounting for the presence of the necessary pollinators—the gall-wasps. It does not seem possible for these tiny delicate insects to traverse the 200 miles of sea or more, and arrive safely at a distant island. The genus is absent from the Hawaii Islands, but there is a species in Fanning Island, 900 miles south, and it is absent, too, from Cocos-Keeling Island, 700 miles from Java. Most of the Polynesian islands, however, possess one or more species.

Could the larvae in the gall-flowers pass uninjured through the intestines of birds, say, a pigeon, which had eaten the fig? If they can, the insects must have perished long before the seedlings had attained a sufficient size to bear figs. I can only suggest that the gall insects can be transported safely in the viscera of the bird, and that the pigeons must have visited the islands on more than one occasion, first bringing the seeds, which grew into trees, and years later bringing the gall-insects, which then fertilised the figs on the now adult trees. I have little clue as to how long these adult insects live, but from Cunningham's account of the fertilisation of *F. Roxburghii* (*Ann. Bot. Gard.*, i, appendix), I gather it is only a few hours. He gives evidence that they can fly ¼ of a mile.

The place of origin of the genus *Ficus* seems to have been the tropics. Of the genus *Dorstenia*, in Africa there are about 50 species, and South America 20 species, and 1 species also occurs in India. This genus is usually herbaceous, but occasionally shrubby. The inflorescence consists of a flat receptacle, edged with bracts, which is covered above with a mass of minute male and female flowers mixed together. The inflorescences are axillary, and the leaves resemble to some extent those of figs, and are often lobed in the same way as those of the plants of that genus. In the same area, tropical Africa and South America, occur also a few trees or shrubs of no great height, known as *Trymatococcus*. These have the inflorescence as in *Dorstenia*, but the receptacle is pear-shaped, edged at the top with small ovate bracts, like those on the mouth of a fig. In these the flat top is covered with male flowers with a single female flower in the centre, which eventually develops into a rather large drupe, covered by the receptacle in which the ovary was previously embedded. The foliage again closely resembles that of certain species of *Ficus*, being dentate and cuspidate at the tip.

To derive the fig from either of these genera, or from a plant closely allied to them, merely entails that the receptacle, at first flat or concave, bears mixed male and female flowers, or male flowers at the outer edge and female flowers

in the centre. The flowers are then attacked by a species of *Cecidomyia*, which produces galls in the ovaries of some of the female flowers and, in their escape, play the part of fertilisers. The receptacle becomes pyriform, that is, cup-shaped, with an opening in the centre—i.e., at the top—and a fig is formed. Without the fig-insects a fig cannot be fertilised, as the exposed flowers of *Dorstenia* and *Trymatococcus* can be, either by wind or by insects walking over the receptacle, or seeking honey on it, and it is possible that the attack of the gall-wasps prevented the full expansion of the receptacle. In some such way it would seem that the fig was formed.

In an allied genus, *Sparattosyce* (1 species in New Caledonia) the receptacle is actually at first pear-shaped, with an opening at the top, just as in figs, but during flowering this splits and expands, and then resembles that of *Dorstenia*. The male receptacle bears a great number of large flowers, the female from 4 to 6, the long stigmas of which project from the upper opening, showing that they are fertilised by wind or passing insects. In some species of *Ficus* also the figs contain only male or only female flowers.

The genera allied to *Ficus* as now existing are found in very limited areas, while the figs occupy as extensive a distribution as is possible for a genus which requires a warm or hot climate, and have succeeded, and still succeed, in pushing themselves into every unoccupied portion of the globe suited for their habitation, as is shown by the fact that in Krakatau no fewer than 6 species had settled in that island in 23 years (i.e., by 1906), 3 of which were established in 14 years, and 6 more had become established by 1919, a larger number of species than in any other genus. It should be pointed out, moreover, that they would require some years to develop to a sufficient size for identification, and presumably were actually fruiting by the time recorded. The cause of this can only lie in the fact of the evolution of the fig from a flat receptacle, with the achenes exposed, and merely dispersed by the contraction of the withering receptacle expelling the achenes, as in *Dorstenia*, or with the solitary seed enclosed in the remains of the receptacle and forming a drupe, as in *Trymatococcus*, to a berry-like fruit enclosing a large number of small seeds, very well suited for the consumption of bats and birds, which conveyed large numbers of seeds to remote and suitable spots for germination. This evolution could only have been possible with the aid of the little gall-making wasps, for without their aid in pollination the fig could never have attained its present form.

The figs are found in all warm and hot countries, from Southern Europe, over a large part of Africa, tropical Asia to China, and especially abundant in the Malay region (there are 80 species in the Malay Peninsula), Australia and Polynesia, but, as mentioned, absent from Hawaii. There is a specimen apparently of *F. retusa* from Hawaii at Kew, but probably an introduced plant. In America they go as far north as Florida and the Bermudas, and are plentiful in South America. They occur in nearly all tropical islands, except remote coral atolls, and in Krakatau, after the eruption of 1883, 12 species had established themselves by 1919. They are absent mainly from cold regions, and absent or scanty in dry and desert areas, but are most abundant in the tropical rain-forest region, chiefly in the more open country and on forest edges, banks of streams, and such places.

They occur both as terrestrial plants and epiphytes, and frequently commence life as epiphytes, the seeds being deposited by birds or bats in the fork of a tree. Here they germinate and grow, wrapping the trunk of the tree in a network of roots, and eventually killing it. A few species are climbers clinging to tree-trunks after the manner of ivy. In one series the figs are borne on long shoots embedded in the ground. These have dull inconspicuous figs, and are probably eaten by ground-game, pheasants and such birds, or by mammals, rodents or pigs.

The figs on the smaller shrubs, such as *F. urophylla*, *F. diversifolia*, *F. alba*, are small and orange- or yellow-coloured, or occasionally red in *F. alba* when ripe. On the low climbers, *F. punctata*, *F. apiocarpa*, the figs are large and orange- or crimson-red. In a few species, *F. pisifera*, etc., they are white, small and fairly conspicuous. On the bigger trees they are usually green or brown, turning more or less purplish (*Ficus Noronhae*, *F. polysyce*, *F. Miqueliana*), and of fairly large size, ½ inch or more through; or small, entirely purple or black, *F. benjamina*, *F. retusa*; or sometimes, *F. dubia*, rather large, and orange. Very few are too large to be carried off or swallowed by birds. The biggest are *F. Beccarii*, of Borneo, a climber, *F. punctata*, similar but smaller, both orange-red when ripe, and *F. Roxburghiana*, dull pink.

The figs on the shorter shrubs, and conspicuously coloured, are naturally dispersed by bulbuls and other small birds; larger figs, of a dull inconspicuous green, like *F. polysyce*, by bats. Fruit-bats do not fly low; the smaller ones (*Cynopterus*) often feed on trees 15 to 20 feet tall, but not shorter; *Pteropus* only on trees 30 feet tall and higher. In the larger-sized trees, like *F. benjamina* and *F. retusa*, the small black or purple pea-shaped figs are produced at times in vast abundance, and in the daytime are visited by myriads of birds, and at night by numerous fruit-bats, large and small, and also by civet-cats. I have records of 23 kinds of birds and about 10 kinds of fruit-bats which habitually feed on figs, but these are only a small part of the number of species which do so. Nearly all kinds of fruit-eating birds crowd in hundreds to a fig tree in fruit, but, owing to most of the trees being inhabitants of tropical countries, and little known specifically to ornithologists, there are comparatively few records. The ornithologist in tropical countries seldom examines the contents of the crops of the birds he shoots, and too frequently does not record anything of their food. Botanists also, though recognising the plants, are frequently quite ignorant of the names of the birds they see feeding on the fruits.

Anyone residing close to a big tree, say, of *Ficus benjamina*, when the figs, which are black and about as big as a black currant, are ripe, will be astonished at the vast number of birds which flock to it by day and keep up an incessant chattering and twittering, only dashing away when a hawk comes up to catch one, and returning immediately it has gone. At dusk all disappear, and their place is taken by innumerable fruit-bats, chiefly *Cynopterus*, and, if any are in the neighbourhood, the big Fox-bats (*Pteropus*) also come, and keep up a perpetual squeaking and fighting as they feed on the figs. This goes on for some days till all the figs are eaten. The birds are chiefly bulbuls and barbets, but in the Malay Peninsula the Green Pigeon (*Treron vernans*) usually comes in great flights to one of these small-fruited fig trees, as is well known to sportsmen, who get large bags of them as they fly to and from the trees. All these birds and bats fly for considerable distances every night to roost, and consequently carry the seeds of the figs for a mile or two at least.

The larger green or brownish inconspicuous figs borne on the trunks and boughs of trees, as in *F. polysyce*, are eaten by bats only. In that species the figs are dull green, occasionally turning a dull red colour, about 1 inch long. They are borne on very short branchlets on the bare trunk and branches, so close-set that the trunk and branches are covered completely in parts with them. I watched for some time one fine tree in Singapore Gardens when the figs were ripe, and did not see a bird ever touch them, and, as there were then very few of the large bats about, the fruit fell on the ground at the foot of the tree, where they would decay, emitting at the same time clouds of the small gall-wasps. A smaller tree near my house was regularly visited by *Cynopterus marginatus*, which flew up to the tree and carried a fig off to a distant point, ate it, and flew back for another till all were gone. Seedlings

came up in hedges or beneath trees everywhere from the dispersal agency of these bats.

It will be observed that the fruit-bats are very important dispersers of the figs, though by no means the only agents in this work, for birds, especially pigeons and bulbuls, are very assiduous disseminators as well, especially of the smaller-sized figs. The larger bats (*Pteropus*) fly very long distances and migrate, especially in the breeding season, in great numbers. In the limestone caves in Selangor and elsewhere the *Cynopteri* roost by day in enormous abundance, flying out at dusk and scattering all over the forest in search of fruit. Where there are no caves or buildings, they roost during the day in trees. They feed voraciously, passing the excreta very rapidly, but do not eat their fruit on the tree where they gather it, if the fruit is of any size. They fly off with it to another tree.

The long-distance dispersal of figs is, however, mainly effected by birds, chiefly pigeons. In Krakatau, after the vegetation was destroyed by the eruption in 1883, fig trees appeared very soon, as I have shown on page 435. All were widely-distributed species, and were rather small trees with fairly large, plain green or inconspicuous figs, *F. fistulosa*, *F. hirta*, *F. hispida*, *F. leucantatoma* and *F. toxicaria* and *F. fulva* (in this latter the fruits are orange and the plant a low shrub). Except the last, the figs are not of the kinds that birds would be likely to eat, so far as I have seen, but are sought after by bats.

Ernst (in the "New Flora of Krakatau") seems inclined to refer the introduction of these plants to birds, but does not mention seeing any pigeons or other birds likely to have brought them, while he *does* record the abundance of Flying-foxes (*Pteropus*) on the Java coast at no great distance from the island (25 miles), an easy flight for these bats. (I have seen no account of the new fauna of Krakatau, a study of which would have been of some importance.) There is a species of *Pteropus* in Christmas Island, as well as 2 kinds of pigeons, and 2 species of *Ficus*, the very widely-distributed *F. retusa* ranging from India to China and Australia, and very popular with birds, and *F. saxophila*, with yellow or crimson-scarlet figs. In Fernando de Noronha the local fig, a big tree, had figs 1 inch through, green spotted with purple or all purple. There were no bats on the island, and as the fig occurred all over the group, doubtless it was dispersed by the local pigeon, or perhaps the small *Vireo*.

The fig trees of the Polynesian Islands seem all to be trees with small fruits, the biggest, about ½ inch through, and, where described, are of a red or orange colour, suggesting dispersal by birds rather than bats. (Guppy says very little about bats as dispersers of seed, suggesting that they do not carry seeds internally, but that they may disperse the small seeds of *Geissois* by attachment of the seeds to their fur.)

The Pineapple (*Ananassa sativa*) of South America is another and distinct form of compound fruit. The whole mass consists of a part of the stem with a large number of axillary flowers, sessile and bracteate. When ripe, the stems, bracts, calyx and fruits become soft and juicy, forming what is popularly known as a "pineapple." The whole spike is borne on a longer or shorter stalk from the centre of the large tuft of leaves, and, continuing to grow above the flowers, bears a tuft of leaves at the top. The seeds are very small. The wild forms and allied species have the ripe compound fruit of a bright and conspicuous red colour. It is apparently dispersed by animals such as the peccary, or possibly rodents. I have no evidence that birds eat it in a wild state, in spite of the fact that it is so brightly coloured, suggesting the action of birds. The cultivated pineapple is propagated entirely by cuttings from the base or the top tuft of leaves, as the seeds have been lost by cultivation.

Among the polycarpellary fruits we have a number of plants in which the carpels of a single flower form a compact, fleshy, juicy mass attractive to birds, such as *Rubus*, *Fragaria*, all forming small-sized and conspicuous fruit of black, red, or orange colour, *Rubus* being a particularly widespread genus, as has been mentioned. In most of the *Anonaceae* the separate carpels are juicy, coloured, and freely eaten by birds and bats. In *Anona* the carpels form a compact, fleshy, often juicy mass of some size; too big to be carried off by birds, these are generally dispersed by mammals. In *Talauma* (*Magnoliaceae*) the carpels are woody, and dehisce, exposing a seed in each, with a juicy coloured aril attractive to birds. In *Aromadendron* the carpels are connate in a mass, fleshy, about 3 inches long, and of an inconspicuous green colour; these fruits are dispersed by monkeys, who tear the fruits to pieces and scatter the seeds or carry them to some distance.

PART IV

DISSEMINATION OF DRY SEEDS AND GRAIN BY GRANIVOROUS BIRDS

It seems certain that some at least of the small dry seeds of herbs, and grains of grasses and *Cyperaceae* are distributed to some extent by the grain-eating birds which feed on them, although in the great majority of cases the seed or grain is bitten up, or is completely destroyed by digestive processes, as to be non-germinable. Most of the agricultural works and volumes written on the food of useful birds, both in Europe and North America, lay great stress on the value of the finches and other granivorous birds as destroyers of weed-seeds, and their use to farmers in eradicating weeds from their fields. This class of small dry seeds, grains and achenes, is mainly dispersed by rain-wash, wind, and the feeding of herbivorous mammals, which pass the seeds of the herbs they eat unharmed in their excreta. Some are also dispersed by adhesion, due to viscidity, to fur or feathers, or in mud adhering to the feet of birds, or man or animals, carts, etc., or by transportation in soil, or some such ways, but none of these methods will entirely account for the distribution of such plants. They seem hardly to account for the rapid spread of some weeds over a large area, nor for the appearance of such plants as *Panicum*, *Paspalum*, *Eleusine*, etc., in oceanic islands such as Christmas Island, where I have found 2 indigenous species of *Panicum*, the presence of which is difficult to account for except by transport in some way by birds.

It is always possible that birds may pick up small seeds of this type in the sand or grit which they take for digestive purposes, and eventually pass them unharmed.

I have examined a certain amount of the excreta of sparrows and other finches, but, except in one case, found no seeds which were not entirely destroyed; still, it is shown by Collinge that birds of this type do frequently pass weed-seeds unharmed, and are not so beneficial to the farmer as may appear. The destruction of granivorous birds by hawks, while their crops are still full of uninjured grain, is to be taken into account, and is referred to elsewhere. A good deal more research is required into this question, but I give here what information is available at the present time.

W. E. Collinge has published notes on the subject in the *Journal of the Board of Agriculture, London*, 1913, xx, 15, and in "The Food of British Birds," ed. ii, 325. He quotes Judd ("Relations of Sparrows to Agriculture," *U.S.A. Dept. Biol. Survey* 15, 1901, p. 1), and also Beal's writings, to show the enormous amount of seeds of weeds devoured by sparrows and other finches. Judd made some experiments with English Sparrows (*Passer domesticus*), which he fed on the seeds of climbing false Buckwheat (*Polygonum scandens*), Rag-weed (*Ambrosia* sp.), Lamb's Quarters (*Chenopodium album*), and Amaranth, Millet, Pigeon-grass (*Setaria viridis*), Crab-grass (*Digitaria sanguinalis*). In all these cases the seeds were crushed by the birds and completely destroyed. (He gives only the American names of the plants, to which I have added what I believe to be the correct scientific names.)

Collinge collected the droppings of several kinds of birds and planted

them on sterilised soil. He raised a considerable number of seeds from them. From the excreta of 3 starlings, in 1911, he grew 27 plants referable to 6 species. He shows that the birds, such as the rook, starling and house-sparrow, and probably many other birds, swallow much less grit and soil in dry years than in wet ones, whence it happens that a larger percentage of seeds passes through the alimentary canal in dry years than wet ones. Farmers state that there are more weeds in arable land after a dry summer than after a wet one, and many are of opinion that the weed-seeds are largely disseminated by birds. He gives the following calculations as to dispersal of seeds based upon his sowings of bird faeces in sterilised soils.

Birds.		*Plants raised.*	*Species.*	*Year.*
Starlings	38	57	6	1911 (a dry year).
,,	38	23	4	1912 (a wet year).
,,	38	32	5	1913.
Sparrows	24	59	4	1911 (a dry year).
,,	24	18	2	1912 (a wet year).

He collected the droppings of the Sparrow (*Passer domesticus*), the Greenfinch (*Coccothraustes chloris*), and the Bullfinch (*Pyrrhula vulgaris*) and planted them in sterilised soil, and obtained the following plants from them :—

SPARROW.—*Plantago lanceolata*, *Cerastium triviale*, *Senecio vulgaris*, *Rumex acetosella*, *Bellis perennis*, *Achillea millefolium* and *Ranunculus repens*.

GREENFINCH.—*Sinapis arvensis*, *Rumex crispus*, *Plantago lanceolata*, *Taraxacum dens-leonis*, *Polygonum aviculare*, *Galium aparine*, *Chrysanthemum segetum*.

BULLFINCH.—*Prunella vulgaris*, *Sinapis arvensis*, *Plantago lanceolata*, *Hieracium pilosella*, *Senecio vulgaris* and *S. Jacobaea*, *Cerastium triviale*, *Sonchus oleraceus*.

He also mentions that in a newly-made garden enclosed by a high fence a number of young Sycamores appeared. As the nearest trees were nearly a mile away, it was concluded that the seeds had been washed off the fence by the rain from some bird droppings. (The seed of the Sycamore seems a very unlikely one for a bird to eat, and I have never seen a bird taking any.) He therefore collected a large supply of droppings from the fence, placed them in sterilised soil, and raised the following plants :—Sycamore, *Acer pseudo-platanus*, *Plantago lanceolata*, *Cerastium triviale*, *Rumex obtusifolius*, *Senecio vulgaris*, *Sinapis arvensis*. (These are all plants mentioned as raised from the droppings of the sparrow and greenfinch, except the Sycamore.)

In dealing with the wood-pigeon (in "Food of Some British Birds," p. 283) he writes :—" A careful examination of large quantities of the faeces " shows that many injurious weeds, such as Charlock (*Sinapis arvensis*), Dock " (*Rumex*), Goose-grass (*Galium aparine*), Knot-grass (*Polygonum aviculare*), are " distributed by this species."

It is probable that the granivorous birds disperse many more seeds or dry fruits than is commonly thought.

Pistone states that the Buntings (*Emberiza Schoeniclus*) (Reed-bunting), and *E. pyrrhuloides*, disseminate *Phalaris canariensis*, *Setaria italica* and *Panicum miliaceum*.

Gatke says that *Pyrrhula erythrina*, in Heligoland, feeds on the achenes of *Sonchus oleraceus*, and the Parrot Crossbill (*Loxia curvirostris*) on burrs and thistles (" Heligoland as an Ornithological Observatory "). The goldfinch is a great feeder on thistle achenes. Kay Robinson says that the Snow-bunting (*Plectrophanes nivalis*) eats the seeds of *Aster tripolium*, of which some achenes might adhere to its feathers by the pappus (Guppy). In examining the excreta

of sparrows, which I observed feeding on the fruits of *Aster novi-belgi* and other garden Michaelmas Daisies, I found all the achenes bitten up and destroyed. It may be doubted if many of these composite achenes ever survive their transit through the body of a bird.

I collected a quantity of the excreta of sparrows beneath the roosts in Kew Gardens, and could not find any seed in the mass, nor, though I kept it watered and turned over from time to time, did I succeed in raising a single plant from it. On one occasion I found a seed of *Thalictrum* and one of some other plant in the excreta of a sparrow. It is very clear, from these few observations, that finches and other granivorous birds may disperse these small herbaceous plants, the seeds or achenes of which they eat in large quantities, to a certain extent passing some through the intestines uninjured. Pistone records that people in Italy often sow the contents of the crops of quails when they arrive and are caught on migrating, and so obtain curious and rare plants. These grain-eaters are also caught by hawks, stoats, etc., or wounded by shooters, and may die at some distance from the place where they have been gathering seeds, and so the weed-seeds may be scattered. The destruction of goldfinches in large numbers by hawks, recorded by Meyer, is to be found under the section dealing with this bird. Other frugivorous birds may swallow minute seeds in taking grit for digestion, and pass them safely. All these possibilities have to be taken into account, but still the question arises: To what extent do the finches and quails and partridges, in feeding on these small dried fruits and seeds, pass them unharmed? The appearance of such herbs as produce this class of seed in such abundance in odd places seems to suggest that they disseminate more than would be expected.

Stuart-Baker records (in the *Journ. Bombay Nat. Hist. Soc.*) that he found in the stomachs of two specimens of *Chloropsis aurifrons*, an exclusively insectivorous bulbul, numerous black seeds of a leguminous vetch-like plant, the pods of which were crowded with tiny blue beetles, and suggests that, in feeding on these beetles, the birds picked up the seeds in mistake for them. This may well be so, but, of course, the seeds could not have been adapted to resemble these beetles and deceive the birds. The accident would be due to the hurry of the birds in feeding. The seeds, however, would not be digested by the bird, but would be evacuated later unharmed.

PART V

THE DISTRIBUTION DUE TO BIRDS

The Distribution due to Birds—Migrations and Wandering Birds, Distance of Flight—Rapidity of Flight of Birds—The Time Taken for Seed to Pass Through a Bird.

WHEN making a study of the most widely-distributed genera and orders in the world, one is struck by the vast number of plants which owe their extensive dispersal area, and their abundance in that area, to the action of birds. A large number of these are natives of cold or temperate regions, and in many cases are confined to the northern half of the globe—Europe, North Asia, and North America; some have pushed down the mountain ranges into the tropics; other species are tropical only, found in South America, Africa and Indo-Malaya. These are, perhaps, the most abundant, as fruit-eating birds are more numerous there.

In the temperate regions the fruit supply is usually confined to one season, so that birds there have to supplement their food by animal food, grains or some other nutriment. In the tropical forests there is almost always a supply of fruits eatable by birds throughout the whole year. Hence we find more regular fruit-eaters in the tropics, both birds and bats.

The first appearance of flowering plants we know of is in the Cretaceous Period, at which time the now temperate northern area was much warmer than at present, and in the Eocene period was tropical, getting cooler in the Miocene, and down to the temperate climate of the Pliocene. Thereafter the area cooled rapidly to the Glacial period, which exterminated such of the tropical or subtropical plants as had survived to that period.

Of the old tropical flora of the Cretaceous Period we know little. Of the Eocene plants we know more, and many of these are baccate and drupaceous plants of orders and genera we now know to be bird-dispersed. Among them are Palms, *Magnolia*, *Ficus*, *Rhus*, *Myrica*, *Cinnamomum*, *Anonaceae*, *Cornus* and *Nyssa*. Some of these are amongst the most widely-distributed genera, but this is not due to their antiquity, as is suggested by Dr. Willis, but to the fact that they were bird-dispersed. Many of the plants of that period are now strictly localised. Such are *Nipa* and *Cinnamomum*, abundant in Eocene days in Europe and now confined to the Indo-Malayan region.

So far as I know, there have been very few remains of fruit-eating birds of that date found, but the abundance of fruits adapted for bird-dispersal strongly suggests they must have been abundant at that time. It is easy to see that, in the case of a tropical or subtropical flora, in a gradually cooling region, eventually becoming arctic, only those plants could survive which had good facilities for migration, and as birds, under these circumstances, would naturally migrate southwards to warmer climates, they would carry the seeds of the northern plants southward. As these early floras seem to have been practically the same in Europe and North America, it is not to be wondered at that the most widely-distributed groups are now found on both sides of the world.

The following list gives a good idea of the immense work effected by birds in dispersal, showing, as it does, the great number of genera and orders of plants of wide distribution in the north temperate zone and the tropics. All, unless otherwise stated, occur in both hemispheres and are bird-dispersed:—

Magnolia (*Magnoliaceae*), *Berberis*, *Mahonia* (*Berberidaceae*), *Sterculia* (tropics only), *Grewia* (*Tiliaceae*) (tropics only), *Ilex* (*Ilicineae*), *Euonymus*, *Celastrus* (absent from South America), *Salacia* (*Celastrineae*), *Rhamnus* (*Rhamnaceae*), *Vitis* (including *Cissus*, etc.), *Rhus* (*Anacardiaceae*), *Prunus*, *Pyrus*, *Crataegus*, *Rubus*, *Fragaria*, *Rosa* (*Rosaceae*) (some of these temperate regions only), *Ribes* (temperate regions), *Eugenia* (tropics), *Myrtus* (*Myrtaceae*), *Casearia* (tropics and subtropics), *Passiflora*; *Cornus* and *Nyssa* (*Cornaceae*), *Sambucus*, *Viburnum*, *Lonicera* (*Caprifoliaceae*), *Vaccinium*, *Gaultheria* (absent from Europe), *Myrsine*, *Ardisia* (*Myrsineae*), *Chrysophyllum*, *Sideroxylon* (*Sapotaceae*), *Diospyros* (*Ebenaceae*), *Symplocos* (*Styraceae*) (absent from Africa), *Linociera* (*Oleaceae*), *Menyanthes* (temperate regions only) *Solanum*; *Piper* (tropics only), *Ficus*, *Trema* (*Urticaceae*), *Empetrum*, *Smilax*, *Polygonatum*, *Streptopus*, *Podocarpus*, *Taxus*, *Juniperus*.

Besides these genera of very wide distribution we have the following large orders distributed nearly all over the world, all the species of which are bird-dispersed :—*Menispermaceae*, *Anonaceae*, *Ampelideae*, *Cactaceae*, *Sapotaceae*, *Ebenaceae*, *Chloranthaceae*, *Myristicaceae*, *Laurineae* (all bird-dispersed except a few with very large fruits), *Loranthaceae*, *Myricaceae* (except *M. Gale*) (absent from Australia only), Palms.

From the Antarctic region, travelling northwards, we have *Pittosporaceae*, *Nertera* and *Coprosma* (*Rubiaceae*), *Leucopogon*, *Dianella*.

The proportion of plants in remote islands with bird-borne seeds really varies according to the distance from the nearest land large enough to carry frugivorous birds. In islands within 200 miles of another island or mainland in which there are baccate or drupaceous plants, the number of species is often large; but the farther away the land is, the scantier they become, as such birds as do carry seeds in their viscera only retain them for a few hours, and so lose them on the way. Furthermore, these frugivorous birds do not fly as far as the waders and sea-fowl, which convey seeds adhering to their feathers and feet only, and frequently colonise distant islands with these.

Most of the very widely distributed of the plants with baccate or drupaceous fruits provide food for a large number of species of birds. I give here the number of kinds of birds which eat and disperse some of the widest-distributed genera, so far as I have been able to list them, but the number, especially of tropical fruits and birds, is doubtless much underestimated.

Rubus	48 birds.
Vaccinium	43 ,,
Ficus	44 ,,
Rhus	34 ,,
Prunus	33 ,,
Morus	33 ,,
Vitis	28 ,,
Empetrum	24 ,,
Juniper	23 ,,
Ilex	14 ,,

MIGRATIONS AND WANDERING BIRDS.

The vast flights of birds of many groups in the north temperate region southwards, on the approach of winter, and northwards again in the spring, has been the study of many ornithologists for many years. Mr. T. A. Coward (in "The Migration of Birds") gives a good summary of this work. The subject only affects us in so far as it is of importance in the dissemination of plants at long distances (apart from the wandering birds), both by conveying internally the seeds of the fruits they have eaten, and by attachment of them

to their feathers. In the Palaearctic region the flights are from Europe southwards as far as South Africa, or from North Temperate Asia (Siberia) south to the Indo-Malayan region in the autumn, and back again in the spring. In the Nearctic region the birds fly from Arctic America to Brazil, and often farther south.

There is practically no transverse migration from Europe to North America (except a migration from Scandinavia to Greenland), and none from tropical Africa to South America, nor from the Antarctic regions northwards. I do not say, however, that no birds have ever crossed, nor do not now occasionally cross, the Atlantic, but occasions on which they do are very rare, and these transverse wanderings are mainly confined to sea-birds. Thus F. C. Lincoln (in "Banded Birds," *Tech. Bull. U.S.A. Dept. Agric.* 32, December, 1927) records the flight of the black-headed gull from Germany to Barbados, kittiwakes from the Farne Islands, Northumberland, to Newfoundland and Labrador, and a tern from Maine, U.S.A., to Nigeria; but the regular frugivorous migrants and the waders do not seem to travel transversely from east to west, but from north to south, and back again, in both hemispheres.

According to Knud Andersen, birds migrate on empty stomachs, and with claws, feathers and beak clean of mud. This statement is, however, strongly negatived by much evidence. I have records that the American swallows feed largely on *Myrica* berries before migrating, and the occurrence of seed in the crops of bird migrants in Cyprus, mentioned by Holmboe, and of Pallas' sand-grouse, when large numbers invaded England in 1883 and 1888, is sufficient evidence that birds do carry food internally on migration.

But even if the majority of migrant birds did not feed, and did carefully clean their feet and feathers before taking flight, and one bird in a hundred omitted to do so, or swallowed a berry or two before it started, that would be sufficient to stock a country or island with any given plant. Nor would this apply to cases of birds accidentally blown out to sea by a gale, nor to habitually wandering birds feeding irregularly over a large area of land, or flying from island to island.

Some birds migrate in numbers quite irregularly. In the Singapore Gardens we used to have flights of paroquets, starlings, and other frugivorous birds, invading the Garden at quite irregular intervals, and feeding on fruits for a time, and then moving away, while duck, chiefly teal, jacana, herons, and cormorants, visited the lake, usually singly or in pairs, flying, after a day or two, to the next piece of water, about 4 miles away.

In the equatorial tropical rain-forest region, however, there are no regular migrations, such as occur in the cold north temperate zones, as there are no seasons, and the food supply of fruit and insects is (except during an occasional spell of dry weather) equally abundant throughout the year. Except in the case of the northern migrant waders, which come down from the north in the middle or latter end of the year, there are few seasonal migrants. The only ones I knew of in the Malay Peninsula were the Shama (*Cittocincla*) and the Ant-thrushes (*Pitta*), which only visited the Gardens at certain periods. The Jungle-crow (*Corvus enca*) used to visit the Gardens when the fruits of *Trichosanthes* were ripe, and, as above-mentioned, the Green Starling (*Calaenas chalyboea*), the Paroquet (*Palaeornis longicauda*), and the Myna (*Graculus javanica*), came at somewhat irregular periods in large flocks.

According to Forbes ("Naturalist's Wanderings") the yellow Weaver-bird (*Ploceus hypoxanthus*) often flies to Cocos Island, most probably from Java (700 miles) to nest, and then flies back again. It is difficult to see why this bird should migrate like this.

Many birds seem never to leave the locality in which they were hatched, so long as they can find a sufficient supply of food and are not frightened

away. This is best shown by watching abnormally coloured specimens. I have seen variegated blackbirds, robins, and hedge-sparrows persistent in the same spot, within a radius of 20 or 30 yards, for several years. They move about in the neighbourhood, according to food supply, but always return shortly. Another class of birds, especially in the tropics, moves about the forests, gathering fruits as they go, and evacuating the seeds later at a considerable distance from the food-plant. Social birds such as crows, like fruit-bats, have roosts to which they return regularly at certain times after feeding, carrying with them the seeds of the fruits they have eaten, and evacuating them during their resting period. They may travel from 3 or 4 miles to 10 or 20 miles from the roost.

Hornbills and pigeons, in the tropics especially, travel across far-stretching areas of forest, often crossing arms of the sea, coming down to feed when attracted by the sight of a fruiting tree, and moving on when the fruit is cleared away. The distance they travel is often very long. Marsh (in "Man and Nature") says:—"Pigeons were shot in Albany, New York, a few years "ago (writing in 1864) with green rice in their crops, which it is thought "must have been growing, a very few hours before, at a distance of 700 or "800 miles." The only hornbills I ever saw in Singapore Island were a pair of rhinoceros hornbills which passed over the Botanic Gardens, stopping an hour or so in a large isolated tree, and then passing on in the direction of Western Johor, probably travelling 40 miles or more in the day.

The Waders (*Charadridae*) are the only regular migrants of the tropics, though a good many of the small birds of other orders travel from North America as far south as the Equator. The waders come annually from the nesting haunts in Siberia, and fly as far south through the tropics as they can go. They frequently visit oceanic islands. I have seen birds resembling redshanks and sandpipers in Fernando de Noronha, but they were too shy to procure. In Christmas Island Andrews records that a rail and 8 kinds of waders, including curlew and snipe, and a duck, occur. In Cocos-Island a sandpiper, woodcock, a rail and a teal are known to be found. In St. Helena a Plover (*Aegialitis sanctae-Hollandiae*), said to be endemic, occurs, and a rail is reported. A rail is also said to be found on Tristan d'Acunha.

The distances that many of these birds travel is extraordinary. The golden plover flies from Nova Scotia to South America, 2,400 miles, in a continuous flight, returning by a different route. The only part that these birds can play in dissemination lies in their carrying seeds or small fruits attached to their feet or feathers in mud. Such plants as *Cyperaceae*, *Eriocaulon*, *Polygonum*, Grasses, *Chara*, etc., are conveyed in this way. (An account of dispersal by these birds in this way is given under the account of Isolated Ponds, pp. 543, 546.)

Starting from the north in spring, the waders fly from the muddy spots in or by marshes, lakes, or river banks to a similar spot further south, depositing at the second spot the seeds they brought from the first, and picking up more seeds in the mud. Stopping only at marshy spots, they traverse large extents of country, carrying the seeds of marsh and river plants by stages from north to south and back again on the return flight.

The wide distribution of many of these herbs is due to these birds.

The reef-herons and egrets, which visit distant islands, also carry seeds from place to place, though they do not travel at special seasons. They move about from island to island, and from pond to pond, on the mainland. *Demiegretta sacra* is a wandering bird which has reached Christmas Island and Cocos-Keeling, as has *Herodias nigripes*; and the Night-heron (*Nycticorax caledonicus*) has come to Cocos-Keeling from Australia by Timor. These birds are probably responsible for the occurrence of the *Pisonia* trees in these islands, as they are known to settle in the branches and carry off the sticky fruits attached to their

feathers. Ducks are also long-distance wanderers, sometimes in small flocks, sometimes singly. The Whistling Teals (*Dendrocygna*) fly to Cocos-Keeling, and a duck of unknown species constantly visited Christmas Island, though there was no water other than the sea for it to swim in. These birds, besides carrying seeds in mud on their feet, are fond of eating the fruits of *Potamogeton*, *Ruppia*, *Ceratophyllum*, *Sparganium*, and other aquatic plants, and so transport them as well as by carrying fragments of many species adhering to their feathers. Sea-birds wander irregularly also over large tracts of ocean, carrying the seeds and fruits attached to their feet or feathers (more rarely swallowed) from their nesting-places to remote islands and coasts. The Antarctic Islands, and islands like South Trinidad and St. Paul's rocks, rarely, if ever, visited by any other birds, derive their vegetation mainly through these birds. They fly enormous distances, and the Arctic tern holds the record for long-distance flight of any bird, from the Arctic to the Antarctic regions.

Most distant islands possessing suitable vegetation for their support have one or more endemic frugivorous land-birds which, having once settled there, remain as permanent residents. Thus Fernando de Noronha has a Greenlet (*Vireo*), a Tyrant (*Elainea Ridleyana*), and a Pigeon (*Zenaida*); Christmas Island a White-eye (*Zosterops*), a Thrush (*Merula*), and 2 Pigeons (a *Carpophaga* and *Chalchophaps*); Tristan d'Acunha a Thrush (*Nesocichla*) and a Bunting (*Neospiza*), and so on. Where this class of bird is absent, plants with drupes and berries are also absent. In some islands, e.g., South Trinidad and Martin Vaz, no land-birds are known to occur. The fact that these birds are endemic species (i.e., have so far varied from the original bird which found a resting-place on the island that ornithologists consider them specifically distinct) shows that they have been a long time settled on the island, and in all probability are descendants of a pair or small flock which at some time previously arrived from the mainland. Though it is very probable that the first visitants brought with them some seeds of the baccate and drupaceous plants we find on the island, they certainly could not have brought all. Christmas Island possesses 4 frugivorous birds and 1 bat, and 32 bird- or bat-borne plants. Thus other birds of this type must have visited the island at some time, and we have a report that the Nutmeg Pigeon (*Myristicivora*) has been seen there. It is probable that other birds have flown over from Java, and either perished or returned to their original home. The occurrence of a number of trees of *Spondias dulcis*, in the interior of the island, suggests that the long-flighted hornbills, which carry the seeds of this plant about in Java, have at some time visited Christmas Island. There is now no bird in the island big enough to swallow these large drupes. However (though it is improbable from their inland position) they might have been sea-borne.

Why these small birds go out to sea at all, and, when they do, how they manage to find an island like Christmas or Cocos-Keeling or Tristan d'Acunha, when they apparently fly aimlessly out to sea, or are driven out by a gale, does not seem at all clear. Coward writes :—" Shore birds may rest on the waves. " Sandpipers have been seen feeding as they walked upon the drifting weed " of the Sargasso Sea, and steamers and other vessels frequently provide a " rest for weary birds," and, no doubt, drifting logs, clumps of bamboo, and rhizomes of Nipa, do serve them for a temporary rest. It is very common to see sea-birds settled on this floating drift, but many birds must perish at sea before reaching land.

It occurred to me that perhaps, by ascending high enough on the mainland, a bird might sight the island and steer for it. At what height would the Christmas Island duck require to fly in order to see the island from Java? I am informed by the Astronomer-Royal it would have to ascend for 6 miles.

Now, the greatest height to which birds are known to soar is given by Mr. F. M. Chapman, who saw birds flying at an altitude of 3,000 to 15,000 feet. This seems to be the highest flight recorded. To see an island like Cocos-Keeling, 700 miles from Java, would require an ascent to an altitude of 47 miles or more, which is an impossible height for a bird. Consequently the weaver-birds and teal which fly to Cocos Island could not possibly see the island from Java at from any height to which they could rise. However, though it is low-lying and small, they do reach it, and if they missed it, there is nothing but sea south of it to the Antarctic region.

Distance of Flight.—The distances of flight of some birds during migration are very large, and often accomplished in a surprisingly short time. W. W. Cooke (in "Migration of Birds in North America") states that most birds migrate by night. Ducks and geese, however, travel by day. The smaller birds fly 10 or 12 miles an hour. A purple martin flew from New Orleans to Winnipeg in 12 nights at the rate of 120 miles a night. A night-hawk flew from Yukon to the Argentine, 7,000 miles. The grey-cheeked thrush flew from Louisiana to Alaska (4,000 miles) in 30 days at a rate of 130 miles a day. The humming-birds cross the Gulf of Mexico (500 miles) in one night. The scarlet tanager migrates from Canada to Peru, bobolinks from New England to Brazil. The American golden plover nests in Nova Scotia and flies 2,400 miles to South America without a stop. The Arctic tern is the longest-distance flier known, as it flies from 7½ degrees from the North Pole to the Antarctic regions, practically the whole length of the world, as I have already mentioned.

RAPIDITY OF FLIGHT OF BIRDS.

The rapidity of flight of long-distance flying birds is of considerable importance in the matter of dissemination of seeds, as in the case of islands far from the nearest mainland, if they did not fly sufficiently fast, they would evacuate on the way all the seeds of the last meal they had eaten, before they had reached the island.

In an article in the *Morning Post*, July, 1924, signed "P. Q.," on the speed of birds, the writer says :—" Partridges may fly side by side with a train going " 30 miles an hour." And again :—" Few birds look to be flying slower than " a heron, yet the writer, driving a car at 25 miles an hour, had a heron get up " near the road and beat the car by 50 yards in a distance of about 200 yards." Many distances and speeds of this kind have been accurately measured. Harting (in "Recreations of a Naturalist") tells us of a grouse he saw chased by a falcon, which saved itself by dashing into a plantation exactly 1 mile from where it rose. He timed the flight at 58 seconds, which works out at 62 miles an hour. Again Capt. Gould, a well-known wild-fowler, once stood between two promontories on the seashore, measured to be 1 mile apart, and timed some small lots of teal between the two. The fastest flight took 20 seconds, and the slowest 25 seconds. This means between 144 and 180 miles an hour, and the birds were flying against a light head-wind. He gives, as a general principle, that the larger the bird, the faster it flies. A grouse is faster than a partridge, a blackcock faster than a grouse, a swan faster than a duck. This will only do as a very general principle, for he cites Mr. E. C. Baker, who timed swifts, which he made out to fly at 171·4 to 200 miles an hour.

The rapidity of the flight for measured short distances, and especially if the bird be alarmed in any way, cannot be taken as reliable for long distances of from 250 to, say, 600 miles, as the bird might not be able to keep up the pace for so long.

Harding King (in "Mysteries of the Libyan Desert," p. 90) showed by experiment that the desert doves fed on seeds (probably grass seeds) and olives,

9 hours previously, compared with others similarly fed which had been shot, and must have fed on the olives of the nearest oasis said to contain olive trees, which was 225 miles away, calculated that the latter birds flew at the rate of 25 miles an hour.

Capt. W. S. St. John Hornby, R.N., a great racer of homing pigeons, told me that pigeons can fly 550 miles in 11 hours, from Marennes to Liverpool. Most of these birds can do 30 miles an hour, but some can do 50 miles in the same time, and 600 or 650 miles is as much as a bird can do on end. They fly round when they start, and probably drop their excreta then. Some birds fly through the night, but most usually settle for the dark hours.

By these observations we see the rapidity with which these birds can, and habitually do, fly for long distances. The question next arises whether they can convey seeds internally the whole way.

THE TIME TAKEN FOR THE SEED TO PASS THROUGH A BIRD.

The importance of this point lies in the distance that a bird can carry seed internally, and thus disseminate any species of plant at a longer or shorter distance from the parent plant.

I made some experiments in the Botanic Gardens, Singapore, with birds in the aviary (an account of which was published in the *Journ. of Straits Branch of Royal Asiatic Soc.*, xliv, 265, 1906). A cassowary fed with the fruits of the Coco-plum (*Chrysobalanus Icaco*) at 9.20 a.m. passed the seed after 8 p.m., but before 6 a.m. A hornbill also took the same time as the cassowary to pass the stones of this plant. The Coco-plum is a large-sized drupe over 1 inch through, with a single hard, round seed about ½ inch in diameter. The hornbill, fed with the small berries of *Rhodamnia trinervia* at 10 a.m., passed some of the seed at 12 noon, the remainder at 2 p.m.; thus the last seed was passed after 4 hours. *Myristicivora*, the black-and-white Fruit Pigeon, ate *Rhodamnia* fruits at 10 a.m. and passed all the seed together at 1 p.m.—3 hours. The small damson-like fruit of *Carissa carandas* was swallowed by the hornbill at 7 a.m., some of the stones were passed at 8 a.m., and the remainder at 1 p.m. The *Myristicivora* did exactly the same. The latter bird swallowed the drupes of *Pinanga fruticans* at 8.30 a.m., and began to pass them at 10 a.m., continuing till it passed the last at 4 p.m., the longest period of retention thus being 7½ hours.

It was observed that, when fed with much fruit, the birds passed the seeds much more slowly than when they had but little given them. The *Myristicivora* was apparently not able to swallow the stone of the Coco-plum, nor that of the Rambutan (*Nephelium lappaceum*), and when given a Nutmeg (*Myristica moschata*), merely pecked off the aril. The hornbill swallowed a Betel-nut (*Areca catechu*) complete with the husk on, a scarlet fruit about 2 inches long, but disgorged the seed. As far as I am aware, this fruit is not eaten by any bird in a natural state, in spite of its brilliant colouring. Indeed, I believe the Palm is not known in a wild state anywhere, and, commonly cultivated as it is, I have never seen any plants which seemed to have escaped from gardens, except a few germinating seeds brought down by a stream.

Kerner ("Natural History of Plants," p. 184) fed a thrush on the berries of *Ribes petraeum* at 8 a.m., and it passed the seeds in ¾ of an hour, and seeds of the Elder (*Sambucus nigra*) were found to have passed through the intestine in ½ an hour.

The majority of the seeds with which he experimented took from 1½ to 3 hours to pass through. He says :—" Curiously enough, the small smooth

"fruits of *Myosotis sylvatica* and *Panicum diffusum* were retained for the longest "period."

H. J. Wilson (*American Naturalist*, xxix, 378) fed a Mocking-bird (*Mimus polyglottis*) on various fleshy fruits, and recorded the time of evacuation. He gave 15 seeds of *Yucca aloifolia* : 1 seed was passed after 15 minutes, and the majority after ½ an hour. In a second experiment it passed most of the seeds in ½ an hour, and all within 1 hour.

A bird, given access to an entire Yucca fruit, ate and evacuated 51 seeds in 4 hours. Wilson gave the bird also fruits of *Phytolacca decandra*, *Melia azederach* and *Duranta Plumieri*. Most of the seeds swallowed were passed in considerable numbers in ½ an hour, and the majority in ¾ of an hour.

Sturm fed a large number of different kinds of small birds on the berries of *Adoxa moschatellina*. He found that they passed the seeds in from 15 minutes to 2 hours.

If we estimate the rapidity of continuous flight of a pigeon at 30 miles an hour, and assume that before starting it fed on fruits with small seeds, such as figs, and that it did not evacuate all the seeds for 4 hours, it would convey some in a germinable state for 120 miles. A bird that flew at 50 miles an hour and retained the seed for 7½ hours (the longest period of retention I have evidence of) would convey them for 375 miles. These distances and periods of retention are probably underestimated, as Marsh says that "Pigeons "were shot at Albany, in New York, a few years ago, with green rice in their "crops, which it is thought must have been growing, a very few hours before, "at a distance of 700 miles away." If this observation is correct, as there are comparatively few islands at such a great distance from a mainland or island whence fruit could be obtained by a bird, it is clear that birds may readily convey germinable seed to almost any distant island in the world. As will be seen, however, some distant islands, e.g., Cocos-Keeling, do not contain any plants which possess drupaceous or baccate fruits which could be carried by birds.

The question next arises as to whether birds can or do evacuate the contents of the intestine on passage, or whether they would either evacuate them before they started on their flight, or would retain them till the end of it. Most frugivorous birds evacuate while sitting on a bough or rail. Some ornithologists state that birds could discharge their excreta during flight, and I have certainly seen the blackbirds and other birds do so while flying, especially when startled. The question is of importance for long flights of birds, for if they could, and did so regularly, it would be impossible to account for the presence of baccate and drupaceous plants in remote islands. The fact that such trees or shrubs do occur is some evidence that birds do not completely evacuate the intestine during flight.

Now, it is clear that there is a considerable difference in the length of the periods between the birds experimented on by me and those utilised by Kerner, Wilson, and Sturm. The birds I used were large fruit-eaters—cassowary, hornbill, and pigeon. Those of the other experimenters were small birds. The largest seeds were retained longest, e.g., that of the Coco-plum by the hornbill, 11 hours; the smallest, those of *Rhodamnia trinervia*, the shortest time, 3 hours. Of the other experimenters, the longest retention is given by Kerner, 3 hours, the rest 2 hours or less. I was very particular to record the time of the expulsion of the last seed. I cannot be certain that the other experimenters did the same. A bird that evacuated all the seeds it had swallowed in under 2 hours would not be able to deposit any on a distant island unless it flew exceptionally fast.

The distance of Christmas Island from Java is 194 miles in a straight line. The frugivorous birds there are the Pigeons *Carpophaga Whartoni*, *Chalcophaps*

natalis, and *Myristicivora*, the White-eye (*Zosterops natalis*), and the Thrush (*Merula erythropleura*). The Fruit Pigeon (*Carpophaga*) is allied to or identical with a bird living in Lombok, 1,000 miles away, the Ground-dove (*Chalcophaps*) almost identical with a Javanese species. The other birds are endemic, but probably their ancestors came from Java.

If the ground-dove fed on the figs of *Ficus retusa* in Java and then started to fly the 194 miles to Christmas Island at 50 miles an hour, it would have to retain some of the seeds in its viscera for nearly 4 hours for them to reach the island in a germinable state. The *Carpophaga*, coming from Lombok (1,000 miles) at 50 miles an hour, would have to retain such seeds as those of the *Cryptocarya* and *Sideroxylon* for 20 hours, or to have flown at a much greater rate.

I have given in these accounts of flight, rapidity, duration of time occupied, and periods of retention of excreta, from as much as I personally know and have been able to collect from published works. It is very probable that, scattered through the vast amount of literature dealing with birds, more information is to be found. It has been impossible to effectually search these works for facts. Further research is necessary also. It seems, however, that frugivorous birds can and do visit, or have visited, very many islands at great distances, up to 700 miles, carrying germinable seeds in their viscera. There are certain islands, e.g., Cocos-Keeling, to which birds have, it appears, never brought germinable seeds of baccate or drupaceous fruits (*see under* Island Floras, p. 678), or, to be accurate, no plants with such fruits appear. The greater number of the oceanic islands, however, seem well within the reach of birds from the nearest mainland.

PART VI

LIST OF FRUGIVOROUS BIRDS

I HERE give an account of the birds which eat fruits and disseminate the seeds, arranged in the order in which the groups are classified at the Natural History Museum. It will be noticed that a very large proportion of the different sections of birds play some part in seed distribution, and that carnivorous or piscivorous birds effect a little of this work, and even such groups as the Swallows (*Hirundinidae*), Gold-crests (*Regulidae*), and Titmice (*Paridae*), normally insect-eaters, occasionally disseminate seeds. Many birds eat both insects and fruits. The hornbills, important disseminators of the large fruits of tropical trees, eat small birds, mice, and lizards. In some cases, especially among desert birds, we notice that though they live largely on animal food, they utilise juicy fruits, such as those of *Cacti*, as a water-supply. Certain families, however, are very much more important than others. The *Turdidae*, a widely-distributed family, flying to great distances, even to oceanic islands, disperse small bushes or low treelets; the Pigeons (*Columbidae*)—of especial prominence as tree-seed disseminators in the tropics—the bulbuls, White-eyes (*Zosterops*) and Greenlets (*Vireo*) are general fruit-eaters; the *Dicaeidae*, closely associated with the dissemination of *Loranthi*; the Grouse (*Tetraonidae*), important dispersers of *Vacciniaceae* and *Empetrum* in the Arctic and sub-Arctic areas, are among the most important families of birds. Of the fruits eaten by some families of tropical frugivorous birds we have no information. I have found no record of the food of the *Pipridae*, *Cotingidae*, *Momotidae*, and very little of that of the Toucans (*Ramphastidae*), all South American birds, for I find little bearing on the subject in the ornithologies of tropical America.

In many ornithological works birds are vaguely mentioned as feeding on berries, or having numerous small seeds in their crops, with no clue as to what fruit they fed on. I have not mentioned these as a rule, but only such cases as those in which the genus at least is given. In some of the Indian works and Gosse's "Birds of Jamaica," native names only of the plants are given. I have, however, in most cases been able to identify the plants intended from lists of native plant names. A great deal more observation is required on the fruit eaten by birds. There has been good record work done in Europe, North America, India and New Zealand, but I can find little about the rest of the world.

CORVIDAE.

Corvus frugilegus, the Rook.—This bird feeds largely on grains of wheat and other cereals, of which it destroys large quantities, but it also plays some part in the dissemination of other plants. It carries off and buries acorns, beech mast and walnuts steadily for days, and also carries horse-chestnuts for store to its nest, according to Woodruffe-Peacock (*Selborne Mag.*, xxix, 29). Clement Reid (in *Nature*, liii, 6, 1895, and the "Origin of the British Flora") gives some very important observations on the transport of acorns by rooks. He points out that rooks take acorns in the cups from the trees,

and has seen the acorns pushed into the ground by the birds. He writes (in the " Origin of the British Flora ") :—

" In peat mosses, on open chalk downs, and in ploughed fields, often a " mile or two from the mature tree, one often finds seedling oaks, which last " a few months or perhaps a couple of years, and then die, the conditions not " being favourable." I have for several years noted the position of the seedling oaks, finding them in places where no mammal would take the acorns. For instance, they are common in any of the New Forest peat bogs that are within a mile of an oak tree. They are common also in some places on the top of the escarpments of the South Downs, ½ a mile from oaks, and 300 or 400 feet above them. They are always associated with empty acorn husks stabbed and torn in a peculiar way. In October and November rooks feed in the oak trees, and I have long been of opinion that they were mainly responsible for the dispersal of acorns On October 29th, 1895, in the middle of an extensive field bordered by an oak copse and scattered trees, I saw a flock of rooks feeding and passing singly backwards and forwards to the oaks. On driving the birds away I found hundreds of empty acorn husks and a number of half-eaten pecked acorns. It was noticeable that many of them were not "shed" acorns, but were accompanied by acorn-cups, the stalks of which had been bitten to tear them from the tree. Several uninjured acorns were found; one, almost uninjured, had been driven by a single peck deep into the soft soil of a molehill. In this way oak woods must spread rapidly, but we still want observations as to the extreme distances which acorns are thus carried. I have seen seedling oaks at a distance of a mile from the nearest tree (not necessarily the tree from which the acorns came), and have found the characteristically torn husks somewhat farther away. Mr. J. J. Armistead, moreover, records (*Zoologist*, 1891, p. 19) that he " once found a young oak in a sheltered ravine " among sea-cliffs on the northern coast of Hoy, Orkney. The tree was over " 6 feet high. A few rock-doves bred near the place, and he concluded that an " acorn had been brought by one of these birds, but where from? Unless " it had been picked up on the seashore, it must have been carried indeed " a long way. It could hardly have been brought by man, as the place was " very remote as well as difficult of access." (Guppy shows (" Notes of a Naturalist," p. 571) that very few fresh acorns float, not more than 10 or 12 per cent. in sea-water, and then only for a day or two. Their floating power is due to the space formed by the shrinkage of the kernel after drying, and such acorns found in sea-drift would not germinate.) " Rooks occasionally cross " the Pentland Firth. The distance of the north of Hoy from the nearest " point where oaks grow, is fully as great as the distance across the Straits of " Dover. It is probably twice as great as was the gap between England and " France at the period when the oak was reintroduced after the Glacial Period."

I myself have found oak seedlings scattered over the Dorsetshire heaths at least a mile away from the nearest tree. There were numerous rooks about on the heath between Corfe and Wareham, where these seedlings were growing. I have seen also seedlings of *Quercus ilex* in Guernsey quite a mile from the nearest tree, evidently carried and planted by some bird.

Reid points out that the acorns found in fields were not "shed" acorns, but were accompanied by the cups, the stalk of which had been bitten through. Acorns in cups are more easily carried off by birds (as I have shown they are by squirrels) than the awkwardly large and slippery nut.

J. T. Campbell (*American Naturalist*, xx, 521 and 851) in dealing with the causes of forest rotation, writes of the American crow (the habits of which are given more fully below) as carrying about acorns in much the same way as the rooks do in England, and I add his note here to complete the story of the transport of acorns by this class of birds. " As a crow leaves an oak he " will pluck an acorn, which he may carry away 5 miles, and alight on a beech

"tree, where something may attract his attention, when he drops the acorn "and pecks a cluster of beech nuts, and flies away with it somewhere else."

This is equally likely to happen with rooks or jays, or such acorn-eating birds. When a bird of this type accidentally drops a fruit, it seldom, if ever, so far as I have seen, descends to pick the same one up again.

Pistone says that, thanks to wild pigeons, *Quercus macedonica* and *Q. aegilops* are spread in Sicily and Sardinia; but it is equally likely, and indeed more so, that this is effected by rooks or jays, both of which plant the acorns in the ground where they could readily grow, while pigeons either merely drop them accidentally, or, having swallowed them, are killed by a hawk, and the acorns are only scattered on the ground. A. Pistone (in "Disseminazione zoofila per Uccelli fitofagi," *Naturalista Siciliana*, 1898, 221) says that rooks in Sicily eat the fruits of *Opuntia vulgaris*, *Prunus avium*, *P. armeniaca*, *Olea europaea*, *Pyrus communis*, *Ficus carica*, *Ceratonia siliqua*, *Phoenix dactylifera*, *Chamaerops humilis*, *Zizyphus*, *Berberis*, *Cornus mas* and *Vitis vinifera*.

In times of scarcity in England the rook eats hips (*Rosa*) and haws (*Crataegus*), and, in Sweden, Holmboe records their feeding on Bilberries (*Vaccinium myrtillus*).

In a paper entitled "J'accuse les Corneilles de participer à la propagation du Gui" (*Gand. Bull. Soc. Roy. Bot.*, xiv, 1909, 85), C. Aigret affirms that the rooks carry the fruits of the Mistletoe on their feet, picking them off the ground in walking, and carrying them to the tops of the trees where they nest, and it is possible that the seeds may thus germinate on the boughs.

Corvus cornix, the Hooded Crow.—Buchanan White writes (in *The Scottish Naturalist*, iii, 27), that J. W. Trail told him he had seen a lot of hoodie crows feeding on berries of *Empetrum nigrum*. Woodruffe-Peacock says it eats hedge fruits, even blackberries; and S. Birger records it as feeding on Bilberries (*Vaccinium myrtillus*). Pistone states that in Sicily it eats the fruits of *Opuntia vulgaris*, *Prunus avium*, *P. armeniaca*, *Olea europaea*, *Pyrus communis*, *Ficus carica*, *Ceratonia siliqua*, *Phoenix dactylifera*, *Chamaerops humilis*, *Zizyphus*, *Berberis*, *Cornus mas* and *Vitis vinifera*. Piccone confirms its feeding on Olives (*Olea europaea*) and *Prunus avium* in Liguria. Heinitz adds to this list of its food, berries of *Convallaria majalis*, *Polygonatum*, *Cotoneaster vulgaris*, *Lonicera periclymenum*, *Juniperus communis*, *Rosa canina* and *R. mollis*, *Rubus idaeus* and *Rumex acetosella*.

Corvus corone, the Carrion Crow.—As far as this bird eats vegetable food, it seems to prefer grass seed to anything else, but it sometimes eats baccate or drupaceous fruits. Miss Lister states that she found numbers of pellets ejected by the bird in the Jura, which were composed of cherry-stones, and Woodruffe-Peacock says that crows eat hedge fruits, including blackberries.

In Liguria, Piccone found it eating Olives (*Olea europaea*). In Kew Gardens, where a few are always about, I have seen a pair feeding on the drupes of the Service tree (*Pyrus sorbus*), and have also seen one flying off with a fruit of *Pyrus baccata* in its beak; another was seen carrying off a fair-sized apple. I have also seen one feeding on the fruits of a Lime tree (*Tilia platyphyllos*), from which it was chased away by a jay, who was engaged also in eating these fruits. However, it seems to spend its time chiefly in gathering small seeds in the grass, and eats very little soft fruit, even in hard times. I have never seen it eating acorns.

Corvus corax, the Raven.—This bird apparently eats fruit occasionally. G. Bolan (in "Wild Life in Wales") records finding in its haunts husks of acorns and a cherry-stone. In Sweden, Heinitz has seen it eating juniper berries. Tame ravens are said to bury horse-chestnuts, walnuts, and acorns, and it is possible that wild ones do so also. Holmboe records its feeding on Bilberries (*Vaccinium myrtillus*), and, in his studies of "Vegetation of Cyprus,"

says he found great quantities of the excreta of birds on the Trigonometrical Cairns of the Cyprus mountains, which excreta undoubtedly originated from ravens, and were quite full of seeds, chiefly of *Ficus carica*, and occasionally olives.

Corvus monedula, the Jackdaw, feeds mainly on grain and dry seeds, but, in Sicily, Pistone records it as eating the fruit of *Opuntia vulgaris*, *Prunus avium*, *P. armeniaca*, *Olea europaea*, *Pyrus communis*, *Ficus carica*, *Ceratonia siliqua*, *Phoenix dactylifera*, *Chamaerops humilis*, *Zizyphus*, *Berberis*, *Cornus mas*, *Vitis vinifera*; while, in France, Chapellier (in " Contribution à l'Etude des Corbeaux en France ") says it eats plums and strawberries, and is especially fond of cherries.

Corvus enca, Malayan Jungle Crow.—This large crow generally frequents the dense mountain forests in the Malay Peninsula, and lives largely on fruit, but it comes down to the lowland forests sometimes, in numbers, when the fruits of the *Trichosanthes* (*Cucurbitaceae*) are ripe, to feed on them. These fruits are as big as an egg, and of a brilliant scarlet colour, containing a large number of seeds embedded in a greenish-black pulp. The climber ascends to the tops of tall trees and over small ones, and frequently, when the fruit is ripe, the whole stem withers and the leaves fall off, causing the fruits to be very conspicuous to the high-flying crows from afar. The Malays call the plant Timun Gagak, i.e., the Crow's Pumpkin.

Corvus splendens, Indian Crow.—Troup says that the fruits of *Prunus Pashia* are eaten by birds, especially crows (probably this species) in India, but not till they are rotten, and that crows eat the fruits of *Celtis australis*. C. W. Mason says they eat figs, fruits of *Cephalandra indica* (*Cucurbitaceae*), *Morus*, *Fumaria parviflora*, Jackfruit (*Artocarpus integrifolia*) and *Prunus avium*.

Corvus macrorhynchus, the Indian Jungle-Crow.—These birds are reported by Mason to eat the fruits of *Ficus*, Mulberries (*Morus*); and, Petch, in Ceylon, says he has seen them carrying off unripe Chillies (*Capsicum minimum*).

It is probably this species of which Van Leeuwen writes :—" The crows in " Krakatau feed largely on Papaya. The fruits are a very welcome nutriment " to various birds, the maws and stomachs of crows shot by Mr. Bartels being " crammed with them." *C. macrorhynchus* is also found in Java, and this note refers to that species.

Corvus jamaicensis, Jamaica Crow.—This feeds on ripening Soursops (*Anona muricata*), the Pimento and fruits of Bitterwood (*Picramnia antidesma*), a tree with scarlet berries (Gosse, in " Birds of Jamaica ").

Corvus tropicus, Hawaiian Crow.—Wilson and Evans (" Aves Hawaienses ") state that this crow feeds principally on the fruits of *Freycinetia* (*F. arborea*). This is confirmed by Perkins, who says, as also Wilson does, that they found the crow's stomach absolutely filled with this food. Guppy adds that on one occasion he observed on a leaf below this plant a fruit-head that had been partly eaten by a bird, and a pellet ½ inch long completely composed of *Freycinetia* seeds.

Corvus australis, the Australian Crow.—Of this, W. B. Alexander (in " The Prickly Pear Naturalised in Australia ") says that the *Opuntias* are dispersed by crows eating the fruit.

Corvus brachyrhyncos, the American Crow.—A very extensive list of the food-fruits of this bird is given by E. R. Kalmbach in " The Crow and its Relation to Man " (*U.S. Depart. Agric. Bull.* 621, 1918, p. 90), the fruits and seeds being taken from the crops of the birds. I give first a list of the baccate and drupaceous fruits :—

Berberis vulgaris, *Fragaria* sp. and *Rosa* sp., *Rubus strigosus*, *Amelanchier canadensis*, *Crataegus* sp., *Pyrus malus*, *Prunus avium*, *P. pennsylvanica*, *P. serotina*, *P. domestica*, *P. virginiana* (*Rosaceae*), *Rhus copallina*, *R. glabra*, *R. hirta*, *R. radicans*,

R. *vernix* (*Anacardiaceae*) (the poison oaks and poisonous ivies seem to be extraordinarily popular with these and other birds), *Ilex opaca* (*Ilicineae*), *Berchemia scandens* (*Rhamnaceae*), *Ampelopsis cordata*, *Parthenocissus quinquefolia*, *Vitis cordifolia* (*Ampelideae*), *Cornus alternifolia*, *C. asperifolia*, *C. florida*, *C. occidentalis*, *C. paniculata*, *C. stolonifera*, *Nyssa sylvatica* (*Cornaceae*), *Lonicera japonica*, *Sambucus canadensis*, *S. pubens*, *Viburnum dentatum*, *Symphoricarpus* sp. (*Caprifoliaceae*), *Mitchellia repens* (*Rubiaceae*), *Gaylussacia* sp., *Vaccinium oxycoccos* (*Vacciniaceae*), *Solanum carolinense*, *S. dulcamara*, *S. nigrum* (*Solanaceae*), *Shepherdia argentea*, *S. canadensis* (*Elaeagnaceae*), *Myrica carolinensis* and *M. cerifera* (*Myricaceae*); *Celtis* sp., *Morus* sp. (*Urticaceae*), *Phytolacca decandra*, *Smilax rotundifolia* (*Liliaceae*), *Peltandra virginica* (*Araceae*), *Potomogeton* sp., *Juniperus virginianus* (also confirmed by Philipps, *Forest Quarterly*, viii, i, p. 1). It also feeds on melon, watermelon, and gourds.

It will be noticed that this crow is very much more of a soft-fruit eater than any of the European species, but it must be observed that baccate and drupaceous fruits are far more abundant in North America than they are in the whole of Europe and temperate Asia together. He gives also a list of the dry fruits and grains which are eaten by this bird. These are probably mostly destroyed by digestion, but uninjured ones may be thrown up in the bird's pellets, and may perhaps also be dispersed by the destruction of the crows by shooting, hawks and owls, and other enemies, the seeds being left where the bird falls. They include :—

Ranunculus sp., *Brassica napus*, *Lychnis Githago*, *Alsine media*, *Saponaria vaccaria* (*Caryophyllaceae*), *Portulaca oleracea*, *Oxalis stricta*, *Malva* sp., *Sida* sp. (*Malvaceae*), *Medicago*, *Melilotus*, *Phaseolus*, *Trifolium pratense*, *Vigna sinensis* (*Leguminosae*), *Diodia teres*, *Galium aparine* (*Rubiaceae*), *Ambrosia artemisiaefolia*, *A. trifida*, *Bidens* sp., *Helianthus* sp., *Taraxacum dens-leonis* (*Compositae*), *Lithospermum* sp. (*Boragineae*), *Verbena* sp. (*Verbenaceae*), *Plantago lanceolata*, *Amaranthus blitoides*, *Atriplex* sp., *Chenopodium album*, *C. ambrosioides* (*Chenopodiaceae*), *Polygonum fagopyrum*, *P. arifolium*, *P. convolvulus*, *P. hydropiper*, *P. lapathifolium*, *P. pennsylvanicum*, *P. persicaria*, *P. scandens*, *Rumex acetosella* (*Polygonaceae*), *Quercus* sp., *Castanea pumila*, *Fagus americana* (*Cupuliferae*), *Cyperus diandrus*, *Heleocharis* sp. (*Cyperaceae*), *Andropogon sorghum*, *Avena sativa*, *Bromus* sp., *Setaria glauca*, *S. viridis*, *Echinochloa crus-galli*, *Hordeum sativum*, *Melica striata*, *Panicum capillare*, *Paspalum* sp., *Digitaria humifusa*, *Triticum vulgare*, *Zea mays*, *Zizania aquatica* (*Gramineae*).

In a figure of the constituents of a pellet thrown up by one of these birds he shows a figure of a seed of a *Polygonum* and an acorn, apparently uninjured, and, as has been mentioned, Barrow records the dry bean of a species of *Phaseolus* as brought to a roost.

Barrow (*U.S.A. Report*, 1890) records the following account of the regurgitation of seeds by crows. " A crow swallowed over 80 seeds of *Rhus radicans*. " In a few moments, and within 40 minutes, it had ejected the seeds, all clean, " polished, and enveloped in a thick coating of sand. Whenever grain or " seed was fed to these birds, they invariably swallowed large quantities of " sand with it, a teaspoonful or more at a time, and washed it down with repeated " swallows of water." Kalmbach says the embryos of seeds are seldom affected by this process, and a large proportion of those disgorged are capable of germination. I have not seen any sand or water taken by blackbirds or thrushes for this process of regurgitation, and the seeds of *Phytolacca* and *Pyracantha* ejected are by no means clean and polished—in fact, a quantity of black or red juice often envelops the mass of seeds.

I have given the full list of fruits recorded as eaten and disseminated by these crows to illustrate the great importance of dispersal by birds generally. Barrow gives an account of a crow-roost near Washington which covered an

area of 12 or 15 acres of second-growth trees. The ground was covered with a deposit, in some places of 1 inch in thickness, of the ejecta of the birds. A pound weight of this (dry) contained 4,764 seeds, and he calculated that the roost of 15 acres must have contained 778,000,000 seeds. Most of the seeds were those of drupaceous or baccate fruits, but those of *Strophostyles* (*Phaseolus*), a bean, are mentioned.

The seeds are brought to the roosts from long distances, but besides these spots the birds drop pellets over their feeding-grounds, which, as Kalmbach says, are more likely to be successful than those crowded between the trees of the roosts. The roosts themselves, however, are often shifted, and this agains leads to further spread of the plants.

The importance of this bird in dispersal in North America seems to be very great. It appears to range across the whole of North America, from the Atlantic to the Pacific coasts, and from the north to Florida. It must, therefore, be largely responsible for the distribution of many of the most common of the drupaceous and baccate-fruited plants over the whole continental area.

Pyrrhocorax (*Fregilus*) *graculus*, the Chough.—" Observer," in *Zoologist*, 1910, p. 48, says that the castings of this bird showed it had been eating barley, and it is probably mainly granivorous. Chappelier states that in France it eats the fruits of *Juniper*, *Vaccinium*, *Myrtillus*, and other berries. Piccone adds that it feeds on *Olea europaea*.

Pyrrhocorax alpinus, the Alpine Chough, is recorded by C. W. Mason as feeding on mulberries in India, and Piccone in Liguria found it eating fruits of *Olea europaea*, *Juniperus communis* and *J. nana*, and of *Pyrus aria*. Heinitz adds *Juniperus macrocarpa*, and *J. oxycedrus* and *J. phœnicea*, *Celtis australis*, *Hippophae rhamnoides*, *Rosa canina*, *Pyrus aucuparia*, *Vaccinium myrtillus*, and *vitis-idea*.

Glaucopis Wilsoni, Blue-wattled Crow.—Of this New Zealand bird Sir W. Lawry Buller writes :—" I have sometimes found its crop distended " with the ripe pulpy fruits of *Rubus australis*, *Parsonsia albiflora* (*Apocynaceae*) " and *Rhipogonum scandens* (*Liliaceae*). It also eats the fruits of the native *Fuchsia* " (*F. excorticata*)."

The *Parsonsia* has capsular fruit with plumed seeds. I suppose the crow eats them unripe, or at least before the pods have dehisced.

Physocorax moneduloides, a small Crow inhabiting New Caledonia. Layard (in " Ibis," xxx, 508) says they feed largely on the Candle-nut (*Aleurites moluccanus*), but they usually crack the nut on a stone to eat the kernel. They may, however, drop the nut at some distance from the tree and aid in its dissemination.

Gymnocorax senex, Papuan Barefaced Crow.—According to C. H. B. Grant (" Report on Expeditions of New Guinea," i, p. 9), this bird feeds on wild fruits and berries.

Heterolocha acutirostris, the Huia of New Zealand, according to Sir W. L. Buller, eats the fruits of *Elaeocarpus dentatus* (*Tiliaceae*), *Coprosma lucida* (*Rubiaceae*), and *Hedycarya dentata* (*Monimiaceae*).

Garrulus glandarius.—The Jay eats extensively of berries and drupes in the autumn. In Kew Gardens, where they are numerous, I have seen them eating the fruits of Hawthorn (*Crataegus oxyacantha*), Rowan tree (*Pyrus aucuparia*), Service tree (*P. Sorbus* and *P. floribunda*), *Cotoneaster bacillaris*, *Vitis Coignetiae* and *Tilia platyphyllos*. Woodruffe-Peacock says they eat hedge fruit and cherries. In Sweden, Holmboe states that it feeds on bilberries (*Vaccinium myrtillus*). In Italy, Campagna says it eats figs and grapes, and Piccone has seen it in Liguria feeding on bilberries and *Arbutus unedo*. In Sicily, Pistone affirms it eats fruits of *Opuntia vulgaris*, *Prunus avium*, *P. armeniaca*, *Olea europaea*, *Pyrus communis*, *Phoenix dactylifera*, *Chamaerops humilis*, *Zizyphus*, *Berberis*, *Cornus mas* and grapes.

Besides these, it eats hazel-nuts, acorns, especially those of *Quercus* Ilex and Beech mast, which also it buries to store for the winter. I watched one burying a beech nut in Kew Gardens. It pecked a hole in the ground, implanted the nut, covered it up with soil, and put a tuft of dry grass on the top. As the birds are very plentiful in the fruit season and not so plentiful later through the winter, I conclude that many go away and are unable to recover the acorns and beech nuts they plant in October, and this may account for many of the young beech and oak seedlings scattered all over the Gardens, though most are due to the energy of the grey squirrels.

Perisorus infaustus, the Siberian Jay, according to Heinitz, eats the fruits of *Cornus suecica*, *Rubus chamaemorus*, *Vaccinium myrtillus* and *V. oxycoccus*, *Lonicera coerulea* and *Pyrus aucuparia*, to which Birger adds *Empetrum nigrum* and *Juniperus communis* as also supplying it with food.

Cyanocitta cristata, the Blue Jay of North America.—F. E. L. Beal gives an account of this well-known American bird (in the *U.S.A. Year Book*, 1896, p. 197). He states it feeds on strawberries, *Ribes rubrum*, *Rubi*, mulberries, *Vaccinium*, *Gaylussacia*, *Prunus serotina* and *P. virginiana*, *Vitis cordifolia*, *Amelanchier canadensis*, *Sambucus canadensis*, *Nyssa aquatica*, *Crataegus*, *Aronia arbutifolia*, *Phytolacca decandra* and the harmless *Rhus glabra* and R. *hirta*, but refuses the poisonous species.

Dendrocitta rufa, Tree Pie.—C. W. Mason says that in India this bird eats fruits of *Ficus*, *Morus* and *Zzyiphus Jujuba*, and Loquats (*Eriobotrya Japonica*) and *Dalbergia Sissoo* (seeds).

Nucifraga caryocatactes, the Nut-Cracker.—This bird chiefly feeds on acorns, beech mast, hazel-nuts and pine kernels (*Pinus cembra*). According to Howard Saunders, it can carry a dozen hazel-nuts (*Corylus avellana*) at once in its dilatable pouch and oesophagus. Like the jay and the rook it stores these fruits underground for the winter. *Pinus cembra* is one of the pines in which the cones do not dehisce, and the bird has to break it open to get at the seeds. Kerner writes :—" I have often myself observed this curious phenomenon (of burying " the seeds) in the case of the dissemination of the Arolla Pine (*Pinus cembra*)." Massart states that in carrying off these seeds in Switzerland it frequently drops some, and no doubt in pecking open the cones it often leaves some scattered about which may germinate. Holmboe says that in Sweden it also feeds on the fruits of *Rubus idaeus* (Raspberry), R. *saxatilis*, *Pyrus aucuparia*, *Vaccinium myrtillus*, *Empetrum nigrum* and *Viburnum opulus*, and Mr. H. G. Houseman reports (in *Country Life*, 1927) he saw a pair feeding on holly berries at Heathfield, Sussex.

Nucifraga columbiana, of North America, feeds on the seeds of *Pinus albicaulis*, of British Columbia, with a non-dehiscent cone, as the European Nut-Cracker does on *P. cembra* (*Prentiss*), and it has also been seen eating *Vaccinium* berries in Idaho by Hart-Merriam.

Pica rustica, the Magpie, seems to eat but little fruit in England. Newstead, however, found a holly seed in the crop of one here, but Heinitz gives a long list of the fruit it eats in Scandinavia, including those of *Rosa canina*, *Pyrus aucuparia*, *Rubus idaeus*, R. *chamaemorus*, R. *saxatilis*, *Amelanchier canadensis*, *Fragaria vesca* and *F. elatior*, *Cotoneaster vulgaris*, *Crataegus oxyacantha*, *Prunus domestica*, *P. padus* (and Birger adds *P. avium*), *Berberis vulgaris*, *Sambucus racemosus*, *Euonymus europaeus*, *Ribes nigrum* and R. *rubrum*, *Rhamnus frangula*, *Cornus sanguinea*, *Arbutus unedo*, *Solanum dulcamara*, *Paris quadrifolia*, *Convallaria majalis*, *Polygonatum verticillatum*, *Maianthemum bifolium*, and *Juniperus communis*, and records as found in the stomach of the bird, or its being known to eat, such dry fruits as those of *Betula verrucosa*, *Galeopsis tetrahit*, *Erysimum cheiranthoides*, *Rumex acetosella*, *Astragalus alpinus*, *Chrysanthemum leucanthemum*, *Stellaria media*, *Vicia sativa*, *Urtica dioica*, *Cannabis sativa* and *Capsella Bursa-pastoris*. Birger, in Sweden,

found it eating berries of *Vaccinium myrtillus*, and *V. uliginosum* and *Empetrum nigrum*, and Piccone, in Italy, found it eating olives (*Olea europaea*).

Pica Hudsonia, which appears to be the American form of the magpie, is said by Kalmbach to eat the fruit of *Shepherdia argentea*, *Sambucus*, *Amelanchier*, *Crataegus*, *Prunus avium*, *Ribes*, *Rhus* and *Cornus* in North America.

PARADISEIDAE.—Birds of Paradise.

Paradisea rubra, the Red Bird of Paradise.—Wallace in the "Malay Archipelago," writes:—"A large climbing Arum (probably *Epipremnum* sp.) bears "a red reticulated fruit (probably a fruit spike) of which the birds are very fond." The hunters use this to bait a trap for the birds. *P. minor* is said to eat figs of the kind called Papajas.

Parotia sexpennis, according to D'Albertis, was found to have the stomach full of nutmegs and figs.

Pardigala corniculata fed on "a species of *Urticaceae*" (perhaps *Laportea*) in company with *Gracula Dumonti*.

STURNIDAE.

Sturnus vulgaris, Starling.—This bird, though it feeds mainly on insects and larvae in England, is a voracious fruit-eater in America, according to the American ornithologists. In hard weather in England I have watched it patiently searching for larvae in the soil wherever the snow did not lie, while around it were abundance of berries which it appeared to ignore. It is a bird which travels a great deal, and I have seen one come on board a steamer in the Mediterranean with other birds of passage. It does, however, feed on drupes and berries to some extent in Europe.

Woodruffe-Peacock (in "In a Fox Covert") says that it brought seeds of *Bryonia dioica* (White Bryony) (*Cucurbitaceae*), and disseminated them in the wood, together with *Tamus communis*, *Anemone nemorosa* and *Fragaria vesca*. R. Newstead (*Journ. Bot. Agric. Suppl.*, 1908) says it eats strawberries and raspberries, and quotes Seebohm as saying it eats Elderberries (*Sambucus*). In Kew Gardens I have seen it feeding on the fruits of *Crataegus oxyacantha*, *C. coccinea*, *Vitis Coignetiae*, *Pyrus baccata*, *P. floribunda*, *P. aria* and *P. rotundifolia*, and it is a very voracious destroyer of cherries, especially during the nesting season, and also eats damsons.

Sturm says that it ate greedily of the fruits of *Adoxa moschatellina* fed to it. In Sweden, Holmboe says, it feeds on *Rhamnus frangula* and *Pyrus aucuparia*.

In North America, where it was introduced in 1890, it has a bad reputation for devouring garden fruits wholesale, attacking the orchards in flocks. E. R. Kalmbach and J. N. Gabrielson (in "Economic Value of the Starling," *U.S.A. Bull.* 868, 1904) say that it feeds on mulberries, drupes of *Amelanchier*, *Prunus virginiana* and *P. serotina*, berries of *Sambucus canadensis*, *Nyssa sylvatica*, *Parthenocissus quinquefolia*, *Myrica caroliniana* and *Rhus toxicodendron*, to which Henderson adds *R. radicans*.

H. F. Lewis ("University of Toronto Studies," 30, 1927) records the occurrence of the following seeds in the crops of this bird, those of *Rumex*, *Polygonum*, *Ranunculus*, *Crataegus*, *Rubus*, *Rosa*, *Prunus*, *Trifolium repens* (flowers as well as seeds, the latter probably swallowed accidentally), *Melilotus alba*, *Rhus typhina*, *Lycopersicum* (tomato), *Viburnum opulus* var. *Americana*, *Sambucus racemosus*, *Ambrosia artemisiaefolia*. The amount of wild fruit eaten by the birds is not large. Its chief food, at least in Ontario, consists of insects and house garbage.

The starling has also been introduced into New Zealand, and G. M.

Thompson (in "Naturalisation of Animals and Plants in New Zealand") says that there it feeds on the hard white berries of *Cordyline australis*, fruits of *Griselinia lucida* (*Cornaceae*) and of *Podocarpus dacrydioides* (*Taxaceae*), *Fuchsia excorticata* and *Aristotelia*.

The bird seems to adapt itself readily to any baccate or drupaceous fruits in any country it happens to be introduced into.

Sturnus malabaricus eats figs of *Ficus* sp. (Mason).

Amydrus morio feeds on the fruit of *Ekebergia capensis* and *Olea laurifolia* in Knysna, South Africa (Phillips).

Amydrus Blythi.—This Socotran Starling is recorded by O. Forbes (in the "Natural History of Socotra") as feeding on the fruits of *Zizyphus spina-christi* and *Ficus salicifolia*. It also eats the fruits of the Dragon's Blood Tree, *Dracaena cinnabari*. He states of *Allophylus rhoidophyllus* that he gathered seeds on Matagoti in the clefts of the rocks, at 2,500 feet altitude, which had apparently been passed by birds, possibly *Amydri*, in large quantities.

Spreo bicolor, the Cape Starling.—J. King (in "Bird Life in the Midlands of Natal," Report of South African Association, 1917, 363) says this bird feeds largely on the Inkberry (evidently a *Phytolacca*), and the spreading of this plant to an alarming extent in South Africa is due to this bird.

Pastor roseus, the Rose-coloured Pastor, is extremely abundant in India, and wanders occasionally as far as England. It feeds largely on grain and insects, but it has been shot at Swansea in the act of eating cherries, and also in the Isle of Wight, feeding on Elderberries (*Sambucus nigra*) (Meyer, "British Birds," iii, 175). In India, Troup says the fruits of the white Mulberry (*Morus alba*) are greedily eaten by this bird, and the seeds are widely scattered, particularly in new-felled coupes, since the birds have a preference for the standards left in the coupes. Stebbing says: "A good example of this action of birds (the "dispersal of plants by undigested seeds) can be seen in the Changa Manga "plantation, where the Rosy Pastor, which assembles in enormous flocks to "feed on the mulberry trees in the plantation, has distributed the seed, and "consequently planted up considerable areas in this manner." It also eats the fruits of *Ficus religiosa*, and Mason, examining the crops of 6 birds, found the seeds in all of them.

EULABETIDAE.

Calornis chalybaea, the Green Glossy Starling, used to visit the Singapore Botanic Gardens irregularly in small flocks, and ate various fruits voraciously. It seemed especially fond of the red drupes of the Palm *Kentia macarthuri* (*Ptychosperma macarthuri*), a native of Australia, cultivated there. These drupes are about ½ inch long, and are produced in large bunches. The seedlings germinated and grew in various parts of the Garden to which the birds carried the seeds, and even outside to a small wood, but they apparently did not carry them more than about 200 yards from the tree. They also joined the bulbuls and other birds at the trees of *Ficus benjamina* when it was in fruit, and ate the small figs.

Rumph (in Herb. Amboin.) says of *Santalum album* fruits, "Sturnorum avide comediuntur." These starlings were either this or an allied species of *Calornis*.

Van Leeuwen states that *C. chalybaea* eats the fruit of *Macaranga tanaria*, a widely-distributed tree, evidently popular with birds.

Gracula javanica, the Talking Mynah, used to visit the Singapore Botanic Gardens irregularly in small flocks. It is a regular fruit-eater, and I have seen it feeding on the round black drupes of the Palm *Oncosperma tigillaria*. Forbes ("Wanderings of a Naturalist") says it frequents the Papaya trees (*Carica papaya*), of the fruit of which it is remarkably fond; and Vorderman, in Java, found seeds of wild figs in their crops.

G. religiosa, the Ceylon Hill Mynah, according to Lewis, eats the fruits of *Adinandra lasiopetala* (*Ternstroemiaceae*) and *Myristica laurifolia.*

Acridotheres tristis, the Indian Mynah.—Of this bird, Troup states that it eats the fruits of *Artocarpus Lacoocha*, and Mason adds the figs of *Ficus religiosa.* Lewis says that the Mynahs in Ceylon (presumably this bird) feed on the fruits of *Kurrimia zeylanica* and *Canarium zeylanicum.*

ORIOLIDAE.

Oriolus galbula, the Golden Oriole, is a migrant bird which arrives late in spring in Holland, Italy, and France, and retires to Africa in August. It is said to feed on cherries, figs, and olives (Meyer's "British Birds," ii, 35), and Pistone adds *Rubi*, and *Phillyrea variabilis* to the list.

O. kundoo, the Indian Oriole, according to Mason, eats the figs of the Banyan (*Ficus bengalensis*), Mulberries and Pakur (*Ficus infectoria*).

O. luteolus, Ceylon Oriole.—Lewis states the orioles in Ceylon nest in trees of *Glenniea zeylanica*, and the fruit of this tree is certainly eaten by birds. He probably refers to *O. luteolus.*

O. indicus, of the Malay Peninsula, feeds on figs of *Ficus benjamina*; and, according to Robinson, *O. cruentus*, of the same region, feeds on fruits of *Melastomaceae.*

Psarolophus ardens, the Red Oriole of Formosa, feeds on various berries, including Figs (*Ficus* spp.) (Swinhoe, "Ibis," v.).

ICTERIDAE.—HANG-NESTS.

Quiscalus quiscala.—This North American bird, according to Henderson, feeds on the fruits of *Rhus radicans* (as does also *Sturnella magna*, the American Meadow-Lark). Hart-Merriam states that it eats Mulberries (*Morus alba* and *M. nigra*). Beal adds the fruit of *Rubi*, *Fragaria*, cherries, currants, grapes, *Vaccinium* and *Gaylussacia*, *Cornus*, *Sambucus*, *Aronia arbutifolia*, *Amelanchier canadensis*, *Celtis occidentalis*, *Rhus glabra*, and other species, and *Myrica cerifera*, as well as chestnut, mast, and weed-seeds.

Icterus leucopteryx, according to Gosse, feeds on oranges, *Pimento* and *Papaya*, in Jamaica; *I. spurius* and *I. galbula* in North America eat Mulberries (*Morus alba* and *M. nigra*) according to Hart-Merriam; and Nelson (in "The Birds of the Tres Marias Islands, Mexico") writes of *I. Graysoni*: "These birds were "frequently seen clinging to the Giant Cactus (*Cereus*) and feeding on the "juicy fruits," and he also records their eating the figs of a species of *Ficus.*

Molothrus ater, the North American Cow-bird, feeds on the Mulberries, black and white (Hart-Merriam), raspberries and *Vaccinium* berries (Beal), but it also is a large weed-seed eater.

Agelaeus phoenicurus, the Red-winged Blackbird of North America, eats the fruits of *Rubi*, *Vaccinium*, *Fragaria*, *Ribes grossularia*, *Symphoricarpus*, *Celtis occidentalis*, and *Myrica cerifera* to a small extent (Beal).

Scolecophagus carolinus feeds on the fruits of *Shepherdia argentea* and *Celtis occidentalis* (Beal).

PLOCEIDAE.—WEAVER-BIRDS.

The Munias (*Munia maya*, etc.) apparently feed on grass seeds only. They were very abundant in open country in the Straits Settlements, and generally fed on the ground in grassy spots, like sparrows; but *Munia tristissima*, of New Guinea, appears to be a berry-eater, for C. H. Grant (in the Reports on the Dutch New Guinea Expeditions of 1910–1913) says: "Only once did

"I observe this little weaver-finch, when a small party of five were feeding "on some small black-berries growing on a shrub."

Ploceus hypoxanthus, the Yellow Weaver-bird, according to Ross, flies across to Cocos Island to nest, probably from Java, 700 miles, and returns after nesting. It might readily bring seeds with it. Sykes records *P. boya*, of India, eating fruits of Figs (*Ficus bengalensis*) (Mason).

TANAGRIDAE.—Tanagers.

These are natives of the New World, and some migrate from North America to Brazil. *Pyranga erythromelas*, the Scarlet Tanager, which eats Mulberries (*Morus nigra* and *M. alba*) (Hart-Merriam), does so. *P. bidentata* was seen, with other birds, swarming on a *Ficus* in fruit in the Tres Marias Island, Mexico, by Nelson. *Tanagra zena*, in Jamaica, feeds on the fruits of the Bully Tree (*Sapota sideroxylon*), and the Fiddle-Wood (*Citharexylon*) (Gosse, "Birds of Jamaica"). The latter genus has several species in Jamaica which have racemes of small scarlet berries.

FRINGILLIDAE.—Finches and Buntings.

The finches and buntings are for the most part dry-seed and grain eaters, living mainly on seeds and achenes, which, in eating, they crush with their strong bills, and finally destroy completely in the digestive process. Hence they were supposed to be valuable as destroying the seeds of crop-weeds; but Collinge has shown that a certain number of these seeds pass through the bird uninjured, and are actually disseminated by them. The dispersal of this class of seeds I have treated as a separate subject; it is one on which a good deal more research is required. Besides these dry seeds, however, many of the finches eat berries, drupes, or other small fruits, of which they digest only the pericarp, and pass the seed itself in a suitable state for germination. This especially happens when the birds are thirsty in dry weather, and in the case of nestlings, which cannot digest the hard grain, and are fed on berries. In an account of the flora of Arizona and California a writer says the Giant Cactus (*Cereus giganteus*) is a very interesting inhabitant of these deserts. Its fruit is very attractive to many species of birds, and, according to Toumey, nearly fifty different birds feed on the fruit of it, "the list including all our Thrashers "(*Harporhynchus*, etc., *Mimidae*), woodpeckers, finches and pigeons." There can be little doubt that it is want of water that induces these seed-eaters to devour this fruit in the desert.

Carduelis elegans, Goldfinch.—This bird is well known as a feeder on the achenes of thistles, Teasel (*Dipsacus*), Dandelion (*Taraxacum*), Groundsel (*Senecio vulgaris*), and other *Compositae*, and is accredited with destroying large quantities of the seeds of these plants which are so objectionable to agriculturists. Thomson (in "Naturalisation of Animals and Plants in New Zealand"), however, states that *Centaurea nigra* and *C. cyanus* are actually disseminated by introduced goldfinches (which are very fond of the seed) in New Zealand, and, W. W. Smith adds, it so disperses *Onopordon acanthium*. Pistone says that in Sicily it disseminates the seeds of *Alyssum maritimum* (*Cruciferae*). Sturm found it would eat the fruit of *Adoxa moschatellina*.

Meyer ("Illustrations of British Birds") records that in a field near the River Thames, in Middlesex, he found a spot 6 feet in circumference entirely covered with the remains of at least 100 goldfinches, which had been torn to pieces by a hawk, probably a kestrel. In such a case the crops of the birds must have contained some recently swallowed achenes, which would be strewn about the ground, and might grow.

Linota linaria, the Linnet.—This bird is also a large eater of dry seeds, achenes, and such-like hard food, but Holmboe records it as feeding on *Chenopodium album* in Sweden, of which it may pass the seeds. I have watched linnets feeding on the fruits of *Poterium sanguisorba* on the Swanage Downs. These small fruits, borne in compact heads, have a soft green calyx enclosing a small black achene. When quite dry, the calyx dries up and forms a wing, which enables the seeds to be dispersed readily by the wind for some distance. The fruits which the linnets were eating were soft and green, but the seed seemed to me to be ripe. The Twite (*L. montana*), according to Sheppard, in Norfolk eats the seeds of *Salicornia herbacea* and *Aster tripolium*.

Passer domesticus, the common Sparrow, feeds mainly on insects till the autumn, as in September I have found the excreta consisting of a mass of elytra and other hard parts of beetles. During the winter they feed largely on the small dry seeds, such as *Amaranthus*, *Plantago*, etc., cereal grains, achenes of *Aster*, *Leontodon*, etc. J. Ritchie (in the *Scottish Journal of Agriculture*, July, 1925, p. 288) gives the following list of seeds and fruits they eat: Knot grass (*Polygonum* spp.), Violet (*Viola*), Chickweed (*Stellaria media*), Spurrey (*Spergula arvensis*), Goose-foot (*Chenopodium*), Yarrow (*Achillea*), Dock (*Rumex*), Groundsel (*Senecio vulgaris*), Sorrel (*Rumex acetosa*), and Buttercup (*Ranunculus*). Heinitz records its eating and passing in a germinable state seeds of *Capsella Bursa-pastoris*, *Rumex acetosella*, and *Stellaria media*. Collinge shows (in "Food of British Birds") that some at least of these dry seeds which it eats pass through unharmed (*see under* Seeds Eaten by Granivorous Birds, p. 439). I have examined a quantity of its excreta, dropped both sporadically and in large quantity, beneath its nest, and except in one or two cases have found no achenes or seeds in a germinable condition. In eating the achenes of the Michaelmas daisy (*Aster Novi-Belgii*), it bit them entirely to pieces. It frequently carries grass bents and other fragments with ripe seed in the panicle, and drops them about as it flies, or beneath the nest (as described under Birds' Nests, p. 512), and this may account for the presence of grass, etc., on high roofs. I have, however, found in their excreta in September an uninjured seed of *Thalictrum* and another seed, unidentified, in Kew Gardens, near a bed of *Thalictrum*, and I saw one bird with a portion of the sweet pithy flesh of the Service Berry (*Pyrus sorbus*), which it had carried to some distance from the tree, and which still contained seeds. It certainly occasionally feeds on juicy fruits. Hart-Merriam reports it as eating Mulberries (*Morus nigra* and *M. alba*) in America, where it has been introduced, and C. H. Hooper states it eats cherries, red currants, and strawberries in England.

Passer hispaniolensis.—According to Campagna, this bird eats strawberries (*Fragaria vesca*), and Pistone says that it aids in the dispersal of the bulbils of *Oxalis cernua*, which, introduced into the Palermo Botanic Gardens, was spread all over the country by these birds. *Passer Italiae*.—This sparrow, according to Piccone, eats black and white mulberries in Liguria.

Gymnorhis flavicollis, Yellow-throated Sparrow of India.—Mason records this as occasionally eating *Ficus* fruit.

Spinus tristis, the American Goldfinch, *Spizella socialis*, the Chipping Sparrow, and *Melospiza fasciata*, all North American finches, according to Hart-Merriam, eat the black and white Mulberries.

Geospiza.—There are 5 species of this genus of finches in the Galapagos Islands. They feed on insects and dry seeds to some extent, but Beebe found them eating the fruits of *Bursera graveolens* (*Burseraceae*), a red cherry-like drupe. This plant is abundant all over South America, from Mexico to the West Indies and Peru, and Gifford (in Proc. Calif. Acad. Sc., ii, 1919) records their eating what he describes as "green tropical plums" in the Galapagos.

Camarhynchus pauper, another finch from the same islands, ate the fruits of

Bursera and those of *Phoradendron*, a parasitic Mistletoe, according to Gifford. It seems probable that the seed of the latter plant was introduced to the islands by this bird.

Fringilla coelebs.—The Chaffinch seems to be mainly an insectivorous bird. It is often to be seen beneath trees bearing fruit, where the drupes or berries are fallen to the ground, constantly at *Ilex verticillata* and some of the North American *Crataegus* in Kew Gardens, though I have not seen it eating the fruit, but apparently searching for insects which come to the decaying fruits. However, it does eat fruit to some extent. Mr. Dymes tells me it eats the fruits of *Tamus communis*, Campagna says it eats the fruits of *Fragaria vesca* in Italy, and Piccone says it feeds on Mulberries (*Morus nigra*). It sometimes eats hawthorn berries. Holmboe records its eating Elderberries (*Sambucus nigra*), and Sturm says it ate the fruits of *Adoxa moschatellina* when he gave them to it.

Fringilla montifringilla, the Brambling, according to Sheppard, eats the fruit of *Polygonum aviculare* and Beech mast in Norfolk.

Pyrrhula vulgaris, Bull-finch.—This bird frequently eats drupes or berries. I have constantly seen it, in Kew Gardens, eating the fruits of *Ilex verticillata*, and also *Cotoneaster rotundifolia*. Collinge says it eats blackberries, elder fruits, currants, and fruits of *Prunella vulgaris* and docks, to which Newton adds those of nettle, while Sturm found it would eat fruits of *Adoxa moschatellina*, and Pistone says in Italy it eats the berries of *Juniperus communis* and *J. nana*, and *Rhamnus frangula*.

Pyrrhula violacea.—This Jamaican species is said by Gosse to eat coffee berries.

P. rubicilla.—In Liguria, Piccone says this bird eats fruits of *Rhamnus frangula*.

P. nepalensis.—This bird is found on the high mountain, Gunong Tahan, in Pahang, Malay Peninsula, where H. C. Robinson found it feeding on fruits of *Leptospermum flavescens* (*Myrtaceae*). These fruits are at first pulpy and black, and later become capsular, with numerous minute seeds. It is possible that the bird may eat them when baccate, and the seeds then may be ripe enough for germination.

Pinicola enucleator, the Pine Grosbeak.—In Sweden, Holmboe records this bird as eating the fruits of *Pyrus aucuparia*. In America, according to Phillips, it eats the berries of *Juniperus virginianus*, and Gabrielson adds the fruits of *Vaccinium*, *Rubus*, *Carex*, *Smilax*, *Montia*, *Argemone*, *Potentilla*, *Fragaria*, *Amelanchier*, *Crataegus*, *Prunus*, *Empetrum*, *Rhus glabra*, *Shepherdia argentea* and *S. canadensis*, *Aralia nudicaulis*, *Cornus canadensis*, *Rhododendron lapponicum*, *Gaylussacia*, *Solanum*, *Lonicera involucrata*, *Symphoricarpus*, *Viburnum*. Some of these fruits and seeds are dry, and hardly likely to be dispersed by the bird.

Carpodacus purpureus, the Purple Finch of North America, feeds on berries of *Juniperus virginianus* and Mulberries (*Morus alba* and *M. nigra*).

Rhynchostrathus socotranus.—According to H. O. Forbes (in the "Natural History of Socotra") this bird's food consists of seeds and small fruits, those of *Croton* and the small red berries of an abundant laurel-like tree being its favourite food.

Loxia curvirostra.—The Crossbills feed mostly on pine seed, and occasionally accidentally disperse it when feeding. Pistone says this bird also feeds on the berries of *Juniperus communis* and *J. nana* and *Rhamnus frangula*. *Loxia leucoptera*, White-winged Crossbill.—J. N. Gabrielson (*U.S.A. Agric. Bull.* 1249, 1924) says this crossbill feeds on *Empetrum nigrum* and *Gaylussacia* berries.

Acanthis linaria, Redpoll.—This chiefly feeds on the seeds of Birch and Alder, but in America is known to eat occasionally the fruits of *Rubus*, *Gaylussacia* and *Viburnum* (Gabrielson).

Plectrophanes nivalis, Snow-bunting.—This chiefly feeds on grass seeds and those of herbs such as *Honckenya peploides*, *Silene acaulis*, *S. inflata* and *Polygonum*; Gabrielson, however, records it as eating the fruits of *Rubi*, *Empetrum*, *Parthenocissus quinquefolia* and *Vaccinium* in America; and Birger says in Sweden it eats fruits of *Rubus chamaemorus*, *Menyanthes trifoliata*, *Ranunculus repens*, and *Chenopodium album*. R. Brown (" Earth and its Story ") found a seed like that of a *Suaeda* in the gizzard of one.

Calcarius lapponum, Lapland Long-spur.—This feeds mainly on grass seeds and other dry seeds such as *Gentiana*, and *Viola Langsdorffi*, but it also eats the berries of *Cornus canadensis*, *Vaccinium* and *Symphoricarpus* (Gabrielson).

Chloridops Kona, a big Hawaiian Finch, is described by Perkins as feeding on the fruits of *Myoporum sandwicense*. Guppy describes a young tree of this plant, 4 feet high, growing in the fork of *Metrosideros polymorpha*, in Hawaii, where its seed must have been dropped by a bird.

Emberiza miliaris, Corn-bunting.—This feeds mainly on grain and dry seeds. Miss E. L. Turner (in " Broadland Birds," p. 111) records seeing the corn-bunting feeding its young on ivy berries.

Cardinalis cardinalis, the Cardinal Bird of America.—These birds, according to Henderson, eat the drupes of *Rhus radicans*. W. L. McAtee (" Food Habits of Grosbeaks," *U.S.A. Agric. Bull.* 22, 1908) states that they generally bite up the seeds in devouring fruit. He gives the following list of fruit seeds found in their crops: *Juniperus virginianus*, *Polygonatum biflorum*, *Smilax bona-nox*, *Celtis mississipiensis* and *C. occidentalis*, *Phytolacca*, *Liriodendron tulipifera*, *Lindera Benzoin*, *Ilex opaca* and *I. glabra*, *Vitis aestivalis*, *V. cordifolia*, *V. rotundifolia*, *Passiflora incarnata*, *Opuntia*, *Cornus* spp., *Vaccinium virgatum*, *Ehretia elliptica*, *Solanum*, *Sambucus* and *Viburnum*.

It apparently feeds like the hawfinch, biting up some seeds and hastily swallowing others.

Eumelodia melancephala, of America, feeds on cherries, mulberries, *Rubi* and *Pruni*, of which they seem to prefer small-fruited ones such as *P. mahaleb*, and *Crataegus Douglasii* (McAtee).

Coccothraustes vulgaris, the Hawfinch, feeds largely on the kernels of fruits, and in this case probably destroys the seeds. Newstead says it feeds on the kernels of hawthorn, Portugal laurel, cherry, plum and yew, but undoubtedly it swallows whole berries, and in this case certainly passes some seeds uninjured.

J. C. Barclay (in Meyer's " British Birds ") states that he saw these birds feeding on the ripe berries of *Mespilus* (*Rosaceae*), and in the winter of 1837-38 on holly berries. Holmboe records it as eating fruits of Rowan tree (*Pyrus aucuparia*) as well as hawthorn, in Scandinavia. In 1925, October, I saw 2 birds at first, and later as many as 5, feeding on the fruits of the Winter-berry (*Ilex verticillata*) in Kew Gardens. They remained for two or three weeks in the neighbourhood, and fed greedily on the berries every day, swallowing the berries whole. They did not reject the skins, as I have seen blackbirds do, but swallowed berries one after the other as fast as they could. Pistone says in Sicily it eats fruits of *Mespilus*, *Crataegus azarolus*, and *C. Isegnae*.

Coccothraustes chloris, Greenfinch.—This lives largely on seeds of field weeds. Collinge has shown that many of these seeds germinate after passing through this bird, viz., *Sinapis arvensis*, *Rumex crispus*, *Plantago lanceolata*, *Taraxacum dens-leonis*, *Polygonum aviculare*, *Galium aparine*, *Chrysanthemum segetum*. Temminck states that it eats Juniper berries. Meyer (" British Birds ") says it pecks at rose hips, and Newstead confirms its eating these. I have seen a flock greedily devouring the small black fruits of *Cotoneaster bacillaris*, a Himalayan tree or large shrub in Kew Gardens (1925). The berries are very small, purplish-green to black, and inconspicuous, but produced in abundance. The birds were at work for

at least a fortnight, for I saw them there on three Sundays. Sturm says it ate of *Adoxa moschatellina.*

Coccothraustes vespertina, an American species, feeds on berries of *Juniperus occidentalis* according to Hart-Merriam, and Gabrielson adds fruits of *Cornus, Sorbus, Symphoricarpus, Rhus trilobata, Ceanothus, Solanum* and *Sambucus.* It, however, splits most of the seeds of these plants, and can open even cherry-stones.

ALAUDIDAE.—LARKS.

C. D. Ekmarck (in an " Essay in Linnaeus, Amoenitates Academ.," iv., 75, sect. viii, 1737) writes : " Sic ager purissimus ab Alaudis aliisque contaminatur " copiosissimis plants aliis Medicagine lupulina, etc., quarum semina pondero- " sissima non venti nec alia adminicula quam solae aves transtulerunt." Under " Alaudis " he includes the skylark and Meadow Pipit (*Anthus*).

Alauda arborea (*Lulula arborea*), Tree Pipit.—Holmboe records this as feeding on the fruits of *Carex, Heleocharis, Polygonum persicaria* and *Empetrum nigrum* in Scandinavia. In " Studies on the Vegetation of Cyprus, 1914," he writes : " A Lark (*Alauda* sp.), was caught on board ship, 27 miles off the coast of " Tunis, quite exhausted, and soon died. Its crop contained 3 seeds of a " Leguminous plant."

MOTACILLIDAE.—WAGTAILS AND PIPITS.

Anthus spinoletta, American Pipit.—This feeds mostly on insects and dry seeds, as all the pipits do, but it is recorded as feeding also on fruits of *Empetrum nigrum* and *Sambucus canadensis.*

MNIOTILTIDAE.—AMERICAN WARBLERS.

Dendroeca auduboni eats the fruit of the Poison Oak (*Rhus diversiloba*) in California. *D. tigrina, D. aestiva, D. castanea,* are all recorded as eating mulberries (Hart-Merriam). *D. coronata,* the Myrtle Warbler, feeds on berries of *Juniperus virginiana* (Phillips), and largely on fruits of *Rhus venenata* (Barrow), and R. *radicans* (Henderson).

MELIPHAGIDAE.—HONEY-EATERS.

The honey-eaters are found in New Guinea, the Moluccas, Australia, New Zealand and Polynesia. Though they feed largely on the honey of flowers, they also eat fruit. Guppy (" Naturalist in the Pacific," 388) says that they eat the Figs of *Ficus* sp. in the Polynesian Islands.

Acrulocereus sp., a Hawaiian bird, according to Perkins, feeds on the fruiting spike of *Freycinetia* (*F. arborea*).

Pogonornis cincta, of New Zealand, feeds on the fruits of *Coriaria sarmentosa* (Buller). *Anthornis lucida,* also of New Zealand, eats the fruits of *Coprosma*

Prosthemadura Novae-Zelandiae, the Tui or Parson Bird, eats soft fruits such as figs and bananas, and also the sugary spadices (and probably also the fruits, as Guppy suggests) of *Freycinetia Banksii* (Buller). J. H. Potts says the nest containing young is sometimes coloured deep purple with the juice of the berries of *Fuchsia excorticata.* In the " Botany of the Kermadec Islands " R. B. Oliver says it eats the fruit of *Melicyrtus ramiflorus, Rapanea Kermadecensis, Myoporum luteum, Coprosma petiolata* and *C. acutifolia, Ascarina lanceolata, Scaevola gracilis, Corynocarpus laevigatus* and the palm, *Rhopalostylis Baueri.*

DREPANIDAE.—Hawaiian Honey-Suckers.

These birds are peculiar to the Sandwich Islands. Perkins ("Fauna Hawaiensis") speaks of some species of Drepanids feeding at times on the red drupes of *Wikstroemia foetida* (*Thymeleaceae*). Wilson and Evans state that the *Psittacorostris* feeds principally on the fruits of *Freycinetia* (*F. arborea*), the seeds being found in its stomach. They also say it is very partial to the berries of some of the tree Lobelias, especially those of *Clermontia*, the seeds passing unharmed in the droppings. These berries are generally yellow, but sometimes bluish in colour, and vary, in the different genera, from ½ to more than 1 inch long.

NECTARINIDAE.—Sun-Birds.

The Sun-birds certainly feed mainly on insects and honey of flowers, but Forbes ("Wanderings of a Naturalist," p. 233) says of a green species of Spider-eater (*Arachnothera*): "On dissection I found its stomach to contain, besides "seeds of *Scitamineae*, a waxy substance. The natives say that it feeds on the "flowers of the *Scitamineae*, which bloom on the ground." The *Scitamineae* mentioned are probably those of the genera *Hornstedtia*, *Zingiber*, etc. The capsules of these plants are often concealed in the coloured bracts, red or yellow, or are themselves exposed and brightly coloured. They are borne close to the ground on the rhizome. The seeds in most have an inconspicuous white aril, which is probably the waxy substance referred to. The *Marantaceae*, e.g., *Phrynium*, have the capsules red, with white arils. It is difficult to see how birds could find the white arils in the dense forest, except such birds as the *Arachnothera*, though perhaps ground-game, such as pheasants, eat these fruits.

DICAEIDAE.—Flower-Peckers.

The Flower-Peckers play the most important part in the dispersal of the tropical and subtropical *Loranthaceae*, and we have excellent accounts of their action in the works of G. M. Ryan, F. Keeble, and Van Leeuwen. Probably most of the species are disseminators of these plants, but the best described ones are *Dicaeum erythrorhynchum*, of India and Ceylon, *D. trochileum*, of Java, *D. cruentatum*, of Sumatra, which disseminates the seeds of both *Loranthus* and *Viscum* (Jacobson, in Robinson and Kloss, "Birds of West Sumatra," *Journ. Fed. Mal. Sta. Mus.*, xi, 202), and *Pachyglossa vinceus*, a species peculiar to Ceylon.

The flower-peckers, however, eat other fruits than *Loranthaceae*, for Ryan states that *Dicaeum erythrorhynchum* feeds on the figs of *Ficus glomerata*, as well as *Loranthus* fruits, and Lewis ("Altitudinal Distribution of the Flora of Ceylon") says that the epiphytic *Medinilla fuchsioides* (*Melastomaceae*) is, he is certain, bird-dispersed, and that he has seen *Dicaeum* hunting along its branches for fruits.

In the *Indian Forester*, xxv, 472, G. M. Ryan gives a very interesting account of the dispersal of the seed of *Loranthus longiflorus* in India by flower-peckers. The plant is parasitic on Teak (*Tectona grandis*) and the Mango Tree (*Mangifera indica*). The fruit ripens in February, and is red-coloured, oblong, and from ¼ to ⅓ inch long. The seed is dispersed by *Dicaeum erythrorhynchum*, a small bird with grey-brown plumage and a short flesh-coloured beak. It holds the fruit broadside in its beak, quickly jerks it round, bringing the blunt end towards its mouth, and presses the pointed end with its bill till the seed is squeezed from the epicarp into its mouth. It swallows the seed whole, leaving the

epicarp in its beak, twisting it about till it extracts all the viscid matter inside it. The whole operation does not last more than 30 seconds. In 8 or 12 minutes from the time of eating, it passes the seed whole, usually without any excrement. Mr. Ryan, who kept one in a cage, watched it for ¾ of an hour, during which time the bird ate and voided 9 seeds; on another occasion it ate and voided 2 seeds in 7 minutes, and in 5 hours 50 seeds. Two or three seeds are eaten in succession and all voided together, and there is, attached to the cluster of seeds, a long film-like substance which helps to make the seeds catch on to the branch when dropped, and become glued there. Some discomfort seems to be felt in passing the seed, for the bird jumps up and down and shakes himself vigorously till he has shed it. He works himself up and down so as to bring the posterior close up to the branch on which he is seated, so that on the thinnest branch of a tree the seed can easily become attached. The seed seems more sticky on emerging from the bird than before entering its mouth, and gets glued to whatever object it touches first. As far as can be judged, it is not the *seed* that the bird cares for, but the viscid coating around it. It is probable that other birds pluck the fruit and suck the viscid coating of the seed (children in the Thana district, Konkan, are very fond of it), but no other bird has been found that swallowed the seed whole.

Ryan wounded one specimen, and it tried to void a seed, and another one shot had 2 seeds (just swallowed) inside. It is thought that as the bird seldom or, according to the people of the district, never drinks water, that there is sufficient water in the viscid coating of the seed to quench its thirst. Ryan also mentions seeing the common grey squirrel eating the *Loranthus* fruit. It did not swallow the seed, but sucked out most of the viscid coating, dropping the seed and epicarp slightly damaged, and he points out that, though a seed in falling might stick to the tree, this would not necessarily spread the parasite from tree to tree.

The extraordinarily rapid passing of the seed by this bird is noteworthy, and would account for the absence of these plants from oceanic islands.

F. Keeble (*Trans. Linn. Soc.*, ser. ii, vol. v, p. 96) also gives an account of the dispersal of these seeds. The two birds in Ceylon which chiefly feed on the *Loranthus* fruits are *Dicaeum erythrorhynchum* and *Pachyglossa vinceus*, a flower-pecker peculiar to Ceylon, the former being known in Ceylon as the "Parasite Bird," as it is so assiduous in visiting *Loranthus* fruits. The smallness of the bird and the largeness of the fruit may together constitute the main reason why the bird has adopted the habit of squeezing the seed of the fruit and rejecting the fruit-coat, and the large quantity of tannin in the fruit-coat may have contributed to this result. In none of the many birds he shot and dissected did the gut contain a fruit coat, though it was generally quite distended with pulpy matter extracted from the fruit. Other birds, however, which visit *Loranthus* fruits do occasionally swallow the seeds, for he shot a Bulbul (*Chloropsis Jerdoni*) whose crop contained several whole fruits of *Loranthus loniceroides*, and in the *Pachyglossa*, of which he dissected about a dozen specimens; in some, pulp only was found (pulp of *L. loniceroides*), and in others pulp with 1 to as many as 3 seeds. Of the seeds so obtained, some (*L. neilgherrensis*) germinated successfully; others, however, were soft and rotten, having been quite killed by the digestive juices. As a rule, it appears that the birds do not swallow the seed except by accident, and Keeble points out that the embryo and endosperm of such seeds as those of *L. neilgherrensis*, *L. loniceroides*, and *L. longiflorus*, and probably of others, are exceedingly rich in tannin, and this may deter the birds from *swallowing* them. He observes that at Hakgala, *Loranthi* are abundant, and on the single telegraph wire there are, every year, hundreds of seedlings of *L. loniceroides* all in early stages of germination. It can hardly be supposed

that the seeds arrive at this anomalous position as a consequence of being voided, but rather that the birds free their beaks of them by rubbing against the wire.

In *Viscum orientale* and *Notothixos floccosus* the viscid layer surrounding the small seeds is less developed. He states that he has frequently found groups of seeds of the smaller *Loranthi*, such as *L. Hookerianus*, in the excreta on leaves and twigs, but such seeds are often quite hollow, showing that the intestinal juices of the bird have played havoc with these tender seeds, though he says in another passage that he has found some germinating.

It will be seen that, as Ryan points out, his observations are at variance with those of Keeble, although they are both dealing with the same bird and with the same species of *Loranthus* in different localities.

The fact of a bird being seen to clean its beak on a twig, after eating the fruit, is no evidence that it is causing the seed to adhere to the tree. I gave a Great Tit two mistletoe berries. It seized the first and bit it, but very soon dropped it, seed and all, and immediately cleaned its beak on the twig of a tree. The second fruit it picked up and threw it down again as soon as it found out what it was.

Van Leeuwen (*Ann. Bot. Gard. Buitenz.*, xxxviii, 1827, 122, "Beitrage zur Kenntniss Javanischen Loranthaceen") says the most common *Loranthus* bird in Buitenzorg is *Dicaeum trochileum* (*D. flammeum*). A caged bird ate only the fruits of *Loranthus pentandrus* (one of the most common Malayan species). When it ate the fruits, it scraped the fruit-flesh and seed off on its perch, and he gives a photograph showing the large number of seeds stuck to the perch. At the end of the day 72 seeds were stuck there. Another species ate the fruits of *Loranthus pentandrus* and *Elytranthe globosa*. The seeds were swallowed and passed. Of 3 fruits of the *Elytranthe* and 3 of *Loranthus Schultesii* swallowed at 2.45, the seeds were discharged at 3.7, and some of the *Elytranthe* swallowed at 3.30 were evacuated at 3.42. This short retention (12 to 22 minutes) would suggest a slow migration of the plants.

We have an account of the dispersal of the seeds of *Loranthus* in Australia by *Dicaeum hirundinaceum* under "Dispersal of Mistletoe," by H. P. C. Ashworth (Field Naturalists' Club, Victoria, April, 8, 1895, quoted in full by M. H. Clifford in the *Indian Forester*, xii, 1). This bird bites the top of the fruit off like a cap, and squeezes the seed into its beak, swallows it, and voids it on a bough. Mason mentions *Dicaeum virescens*, of the Andaman Islands, as feeding on *Loranthus* fruits.

The very thin outer coat of the seeds of *Loranthaceae* certainly would hardly be expected to protect the interior of the seed from injury or destruction by the intestinal and gastric fluids of birds, and the very rapid passing of the seeds, as shown by Ryan, would prevent their being carried to any great distance from the mother-plant. It is, therefore, not to be wondered at, that species of plants of this order are rarely to be found in oceanic islands. The only cases of occurrence of these plants in distant islands that I have found are: *Loranthus Berteroi*, a Chilian species, in Juan Fernandez, and *L. longiflorus* in Timor Laut, where a species of *Dicaeum* and some other flower-peckers occur. It is quite possible that the *Loranthus* in Juan Fernandez, 400 miles from Chile, might have been borne there attached to a bird by its viscid matter, but otherwise the seed must have been retained unharmed in the viscera of some bird for a longer time than is given by Ryan.

Keeble, as stated above, found fruits of *Loranthi* in the stomach of a Bulbul (*Chloropsis*) and I am certain that *Dicaeidae* are not the only birds to feed on *Loranthus* fruits, for in the Singapore Botanic Gardens, and on the roadside trees in the island, *Loranthi* were a perfect pest. Trees had continually to be watched, or they were very soon destroyed by these parasites, the worst of which were *L. pentandrus*, *L. ferrugineus*, and *Elytranthe globosa*.

Now, though *Dicaeidae* did occur occasionally in the Gardens, they were not common, and, indeed, most of the Malay Peninsula species are mountain birds, so that, though I never recorded any observations on other birds feeding on the fruits of *Loranthi*, I cannot but believe that some at least were the disseminators of these plants, and I suspect the common Bulbul (*Otocampsa analis*) was the disperser.

The fruits of *Loranthi* are usually inconspicuous, dull reddish colour, or yellow, but *Lepeostegeres Beccarii* has rather large, shining black berries set off by the brilliant red cone of bracts, while the fruits of the *Viscums* are all white, glutinous, and semi-transparent. The remarkable creeping habit of the seeds of *Elytranthe globosa*, described by N. E. Brown from Dr. Watts's "Observations in India" (*Gardeners' Chronicle*, 1881, July, p. 42) is perhaps suitably mentioned here, though, strictly speaking, it cannot be classed as a case of dispersal. If the fruit falls on a leaf of the *Memecylon* tree, on which the plant is parasitic, the radicle is emitted and fixes itself by a disc; if on a suitable spot for growth, it germinates and develops; if not, the radicle straightens itself and raises the seed in the air, then curves and carries the seed to another spot, where it adheres again; the disc is then released, and, by curving about, transfers the seed to another spot. This is repeated several times, so that it can creep off the leaf to a stem where it can grow. I have several times seen seed of *Loranthus* on a leaf where it had protruded its radicle, which had adhered to the leaf, the seed having been dropped on the leaf by some bird.

ZOSTEROPIDAE.—White-Eyes.

The White-eyes, *Zosterops*, are small, olive-green birds found in Africa, tropical Asia, Japan, Australia, New Zealand and Polynesia. They chiefly feed on insects, but also consume considerable quantities of fruits. They seem to fly long distances across sea, as they often occur in islands some way from the mainland, and one species occurs in Christmas Island, namely, *Z. natalis*, an endemic bird. Andrews, in his monograph of this island, says: "They also eat (besides insects) a good deal of fruit, and "destroy many papayas, custard-apples, and bananas." *Z. lateralis*, the New Zealand White-eye, according to Buller, feeds on the fruits of *Rubus australis*, *Solanum nigrum*, and garden fruit such as gooseberries, cherries, and figs.

T. H. Potts (Transactions and Proceedings of the New Zealand Institute, ii, 1869, p. 40) says: "The *Zosterops* is so partial to the berries of the trailing "*Cotoneaster microphylla* that we have known it taken by hand when busily "engaged on them." It is also recorded as eating the fruit of *Myoporum* sp. by J. B. Cleland (in "The Birds of Pearson Island").

Z. xanthochroa and *Z. griseonota* inhabit New Caledonia, and Layard states that, when the soft berry of *Lantana* is ripe, this is their favourite food; and they really do much mischief by distributing the seeds over great areas. The *Lantana* (*L. mixta*) is a South American shrub, introduced for its ornamental flowers into many parts of the Old World, and the fruit (a small black drupe) is so popular with birds that it spreads all over a country when once introduced, and in planting districts is such a pest that it has been called the "Planter's Curse." It had arrived on Krakatau by 1919, but it does not appear to occur in any other remote islands. *Z. palpebrosa*, of India, is said by Jordan to feed on the blackberries of *Rhamnus* sp. (*Rhamnaceae*), and, according to Mason, on Guavas and figs.

Z. fallax, of Java, is said to feed on *Vaccinium* berries (probably those of

V. waringiaefolium) on Mt. Papandayan, Java, by Van Leeuwen, and *Z. masii* to eat the fruits of *Tacca pinnatifida*.

SITTIDAE.—Nuthatch.

Sitta caesia, the Nuthatch, feeds mainly on nuts and acorns, which it stores for the winter. J. S. Metcalfe (in *Science Gossip*, 1873, p. 34) writes: " On September the 23rd last a nuthatch flew up and, placing something on " a potato mound, gave it several taps with its beak, and then flew off. I " searched and found a small but full-kernelled hazel-nut just beneath the " surface. Soon after I found 6 other nuts buried separately, but not far from " the first. Besides hazel, filbert and cobnuts, he likewise stores acorns and " beech mast." Newstead records this bird as eating seeds of yew, and Portugal Laurel (*Prunus lusitanica*).

PARIDAE.—Titmice.

The Titmice certainly live mainly on insects, but there are records of their being occasionally fruit- and seed-eaters. *Parus caeruleus*, Blue Tit, and *P. major*, Great Tit, are recorded by A. Hibbert Ware as tearing the capsules of Poppies (*Papaver* sp.) to pieces and eating the seeds, and *P. britannicus*, the Marsh Tit, as feeding on the nutlets of *Stachys sylvatica*. Piccone says the Great Tit eats the fruits of *Arbutus uredo*. Harting (" Sketches of Bird Life ") says the Marsh Tit eats the berries of *Symphoricarpus*, and he has seen one carrying off a fruit in its beak. *P. borealis* is recorded by Holmboe as feeding on Rowan berries in Scandinavia. *P. atricapillus*, of North America, is said by Phillips to eat the seeds of *Juniperus communis*.

Chamaca fasciata, the Wren Tit of North America, is evidently more frugivorous. Beal records it as feeding on the fruits of *Sambucus*, *Rhus*, *Rhamnus*, *Symphoricarpus*, *Rubi* and *Lonicera involucrata*, and the Bush Tit (*Psalthiparus minimus*) as eating the drupes of *Rhus diversiloba*.

LANIIDAE.—Shrikes.

Cracticus cassicus, the Pied Piping Crow of New Guinea. C. H. B. Grant recorded (in the Report on the Collections in Dutch New Guinea, vol. i, p. 74) that he saw this bird apparently feeding on berries on lofty trees.

Lanius collurio.—This bird is usually carnivorous, but Sturm gives it as one of the birds which ate fruits of *Adoxa moschatellina*. *Lanius ludovicianus*, of California, feeds on Elderberries (*Sambucus*) and fruits of *Rubi* (Beal, in *U.S.A. Dept. Agric. Bull.* 30, 1907). *Lanius auriculatus* feeds on fruits of *Prunus avium* in Italy, according to Campagna.

Graucalus macii, large Indian Cuckoo-shrike, eats fruits, especially those of the Banyan (*Ficus bengalensis*) (Mason).

AMPELIDEAE.

Ampelis garrulus, the Bohemian Waxwing, is a northern bird occurring in both hemispheres; it inhabits the Arctic regions in summer and migrates southwards as far as Switzerland, occurring not rarely in Britain in cold winters. It feeds exclusively on berries, and especially on the hips of wild roses. Newstead found the crops of this bird full of rose hips in Cheshire. J. Green (in *The Naturalist*, May, 1928, p. 140) noted one eating these fruits and swallowing them whole in Yorkshire. S. H. Waterhouse saw one

feeding on rose hips, also in Yorkshire, and said it seemed to prefer them to anything else, and Holmboe records its feeding on them in Sweden. The latter and Waterhouse say it also eats Hawthorn berries (*Crataegus oxyacantha*), and Waterhouse says it eats elderberries too. In America Dr. Richardson states that it feeds on the berries of *Juniperus*, of the Alpine *Arbutus* (probably *Arctostaphylos alpina*), and the Marsh *Vaccinium* (*V. uliginosum*) as well as the fruits of other northern shrubs. Phillips records its feeding on the berries of *Juniperus scopulorum*, and states that a caged bird ate more than 900 berries and evacuated the seed, between 9 a.m. and 2 p.m.

Ampelis cedrorum, the American Waxwing, feeds on berries of *Juniperus virginianus* (Beal); Parish (" Birds and Mistletoe," *Torreya*, 1905, p. 68) writes: " The Waxwing (*Ampelis cedrorum*) and *Phainopepla nitens* are particularly " fond of a Mistletoe (identified as *Phoradendron californicum*) parasitic on " Mesquit (*Prosopis juliflora*). A fine male *Phainopepla* was secured in Inyo " country. Its stomach was filled with the berries of the mistletoe. A friend " informed me that he has shot the Waxwing and *Phainopepla* when they were " so gorged with the berries that they were extruded on handling." It would appear that in digestion, only the epidermis, and little, if any, of the viscid matter is utilised. The passage through the stomach of the bird serves to remove the non-viscid epidermis, and leaves the sticky coating in a condition for performing its office. Kelly records observing this bird eating fruits of the introduced Barberry (*Berberis vulgaris*) in America.

VIREONIDAE.—Greenlets.

These little birds, resembling our Willow Wrens, inhabit the woods and thickets of South America and the West Indian Islands, and seem to be rather wide wanderers. It is surprising to note the large size of some of the seeds that they apparently readily swallow and pass.

One species, *Vireo gracilirostris*, was one of the three land-birds of Fernando de Noronha where it was abundant and endemic, but allied to a species from the islands in the Bay of Honduras. In the island were an abundance of a big Euphorbiaceous tree, *Sapium sceleratum*, which has small globose capsules ⅜ inch long, containing 1 seed. These fruits and seeds are said to be very poisonous and acrid, but I was informed by the Director of the island that the small birds eat them and pass the seed unharmed, " so that when it rains (he " writes) we meet with little Burra trees (the native name), which are cultivated. " Thus it is well seen that such birds should be very well able to cover in a " short time the whole island with Burra trees as it was once, if it was not " inhabited any more." I have no doubt that the Director was referring to the Greenlets when he wrote, as it was the smallest bird on the island, but it is remarkable that it should eat fruits so poisonous as they seem to be.

V. griseus.—E. A. Chapin (*U.S.A. Dept. Agric. Bull.* 1355) gives an account of " The Food Habits of *Vireonidae*," of North America. These birds, he says, eat fruits in the fall, winter and spring, living on insects during the rest of the year.

The grey *Vireo* eats the fruits of *Myrica carolinensis*, *Morus rubra*, *Polygonum hydropiper*, *Phytolacca decandra*, *Sassafras officinalis*, *Parthenocissus quinquefolia*, *Cornus florida*, *Solanum* sp. *Lonicera hirsuta*, *Sambuci* and *Rhus radicans* (Henderson).

V. Huttoni feeds on fruits of *Rhus* and *Sambucus*; *V. Bellii* on *Polygonum convolvulus*, *Amaranthus* and *Rhus toxicodendron*.

Vireosylva olivacea, which migrates from the Rocky Mountains to Brazil, feeds on the fruit of *Myrica carolinensis*, *Morus rubra* and *M. alba*, *Phytolacca decandra*, *Magnolia foetida*, *Sassafras officinalis*, *Lindera Benzoin*, *Ribes*, *Pyrus*

arbutifolia, *Amelanchier*, *Rosa*, *Prunus pennsylvanica* and *P. serotina*, *Xanthoxylum americanum*, *Rhus typhina*, *Celastrus scandens*, *Vitis cordifolia* and *V. vinifera*, *Parthenocissus quinquefolia*, *Shepherdia* sp., *Cornus alternifolia*, *C. amomum*, *C. asperifolium*, *C. canadensis*, *C. florida*, *C. paniculata*, *Vaccinium*, *Callicarpa*, *Solanum dulcamara*, *Lonicera hirsuta*, *Viburnum*, *Sambucus canadensis*. In Jamaica, according to Gosse (in "Birds of Jamaica") it eats the berries of *Bursera gummifera*, and of Sweet-wood (a name applied to a number of *Laurineae*, *Ocotea*, *Nectandra* and *Acrodiclidium*) and he writes of one: "As it sat it vomited a little white "body, which I found to be the globose seed of a Mistletoe" (probably a *Phoradendron*).

V. philadelphica eats the fruits of *Myrica carolinensis*, *Rosa*, *Vitis* and *Cornus*; and *V. gilva* the fruits of *Myrica*, *Phytolacca*, *Prunus*, *Rhus diversiloba* and other species, *Vitis vinifera*, *Cornus florida*, *C. paniculata* and other species, and abundantly those of *Sambucus*.

Laneovireo flavifrons, of North America, eats the fruits of *Chenopodium*, *Phytolacca*, *Sassafras variifolium* and *Vitis vinifera*; and *L. solitarius* those of *Juniper*, *Smilax*, *Myrica*, *Rhus* and *Berchemia scandens*.

SYLVIDAE.—Warblers.

Most of the Warblers feed on insects for most of the year, but they also eat a certain amount of fruit as well.

Curruca atricapillus, the Blackcap.—According to Meyer, this bird feeds on berries of ivy, elder, blackberries, Dewberries (*Rubus caesius*), and, Wood adds, raspberries. In Italy, according to Campagna, it eats the fruit of the Palm *Trachycarpus humilis*, and Holmboe records its feeding on *Pyrus aucuparia* in Sweden. In his notes on the "Vegetation of Cyprus" he says the blackcap visits Cyprus in September on passage, and numbers are trapped by the natives. He examined the alimentary canal of 56 birds, of which all but 6 were empty, except for the remains of ants. The 6 contained in the intestine seeds of small *Leguminosae* and *Caryophyllaceae*, which, from their position in the intestine, could not have been picked up on the island. Sturm states that it eats the white currant-like fruits of *Adoxa moschatellina*. Piccone, in Italy, found it fed on fruits of *Prunus avium*, *Myrtus communis*, *Hedera helix*, *Viburnum tinus*, *Arbutus unedo*, *Olea europaea*, *Phillyrea angustifolia*, *Phytolacca decandra* and *Morus alba*.

Curruca hortensis, the Garden Warbler.—J. S. Metcalfe (*Science Gossip*, 1873, p. 12) says this bird is a great devourer of small fruits, red currants, raspberries, strawberries and elderberries. Holmboe records its eating the fruit of *Ribes aureum* in Sweden. Sturm states that it ate fruits of *Adoxa moschatellina*.

Sylvia cinerea, the Whitethroat, eats fruits of blackberries (*Rubus discolor*) in England, and *R. tomentosus* in Italy (Piccone, Campagna) and also currants and raspberries (Harting). *S. curruca*, the lesser Whitethroat, eats the berries of *Sambucus nigra*, *S. ebulus* and *S. racemosa*, and the drupes of *Daphne mezereum* in Sweden (*Heinitz*). *S. melanocephala*, in Italy, feeds on the fruits of *Arbutus unedo* and *Phytolacca decandra* (Piccone), and *Rubus discolor* (Campagna). *S. orphea*, in Liguria, eats fruits of *Phillyrea angustifolia* and *Morus alba* (Piccone).

S. salicaria is said by Holmboe to feed the nestlings on the fruits of *Paris quadrifolia* in Sweden, and Sturm found that both the Willow Wren (*S. trochilus*) and the Wood Wren (*S. phylloscopus* var. *rufus*) ate the berries of *Adoxa moschatellina* when offered to them.

Phylloscopus fuscatus, Dusky Willow Warbler of India.—Mason found fig seeds in the crops of 4 out of 22 birds.

Calamanthus campestris, *Acanthiza uropygialis*, *Malurus melanotus* and several of the other Australian Warblers were examined by A. M. Lea, and he recorded

that he found seeds of *Portulaca oleracea* and *Setaria viridis* in the stomachs, together with many insects. It is possible that some of these seeds might pass through the viscera unchanged.

Diaphorilla textilis.—In the stomach of this bird he found seeds of *Erodium cygnorum*. A. M. Lea (" Stomach Contents of Birds," Expedition to North-West of South Australia).

TURDIDAE.—Thrushes.

The Thrushes are among the most important of seed-disseminating birds; indeed, they are only second to the pigeons. Almost all the species feed, at least part of the year, on fruit, drupes, and berries, though many eat animal food as well. They are scattered over the whole world, and some species reach oceanic islands such as Tristan d'Acunha, Christmas Island, and Juan Fernandez. They are often migrants, especially those of the north temperate zone, and are able to fly very long distances, travelling far south in the winter-time.

Merula viscivora, the Missel-Thrush, feeds in the autumn, in England, largely on berries of hawthorn, juniper and yew. I have also seen it in Kew Gardens feeding on the following fruits: *Ilex verticillata*, *Pyrus sorbus*, *P. aria*, *P. aucuparia*, *Pyracantha coccinea*, and *Celtis occidentalis* the American Hackberry. The little inconspicuous orange drupes of this tree seem to be very popular with all the thrushes, as I have seen missel-thrushes, song-thrushes and black-birds all busily feeding on one tree (October, 1925). According to J. G. Wood (Natural History, Birds) the thrush devours the berries of *Arbutus unedo*, as also Piccone says it does in Liguria; and A. Hooper adds holly and ivy berries to the list of its diet. Piccone says in Liguria it eats the berries of *Rubus idaeus*, *Vaccinium myrtillus*, *Juniperus communis* and *J. nana*, and *Prunus avium*.

W. H. Hudson (" Nature in Downland," 1906, p. 228) writes:—" When " the bird has gorged to repletion (on yew berries), he flies to a spot where " there is a nice green turf, disgorges, and then goes back to gorge again. " The result is that every patch of green turf among the trees is thickly sprinkled " over with little masses of disgorged fruit. In a single blob I have counted " as many as 23 whole berries mixed with as many of the green and poisonous " stones." A similar account occurs in an article in the *Times*, October 16th, 1915, on bird gardeners (given by Guppy in " Plants, Seeds and Currents," p. 437), describing the distribution of churchyard yews in Breconshire by missel-thrushes, who drop the undigested seeds on rocky crags 1,000 feet up the mountain slope, where young yews subsequently spring up.

Of *Prunus serotina* J. E. Little (*Journ. Bot.*, 1925, p. 371) writes:—" This " tree is to be found naturalised and self-sown near Peper Harow, West " Surrey." The Rev. W. A. Shaw, who showed the tree to Preb. Burdon and myself in July, 1925, writes on September 21st:—" Crowds of missel-thrushes " are stripping off all the berries as fast as possible, and hawfinches are very " partial to the kernels of the stones, or it would spread more on the common " here." This is a North American tree which has been introduced into England. Its fruits appear to be very popular with birds in its native country, and many species of birds are recorded as feeding on it.

The missel-thrush has been associated with the Mistletoe (*Viscum album*) for many centuries on account of the birds feeding on the berries. Commenius (in Janua Trilinguarum, 1659) says of the thrush: " He is said to dung him- " self a mischief because misselden (bird-lime) sprouteth forth from the bough " which he bedungeth." But it was also mentioned as eating mistletoe berries by Theophrastus, 371 to 286 B.C., and by Pliny and other early authors.

Mrs. E. Horne (in *Journ. Bot.*, 1916, p. 294) gives an account of the method by which the seed is dispersed by these birds. She says: "I was able to watch, "in February last, the manner in which the seeds of the mistletoe are distributed "by the missel-thrush. There were great numbers of the birds present, and they "were eating the ripe berries as fast as they could swallow them. The birds "appear to retain them but a very short time. The digested or partially digested "seeds pass out first, followed immediately by the skins of the berries. The "whole falls in a pile on the bough, the skins forming a protective covering "for the seeds beneath. The gluten contained in the berry is only partly "digested by the thrush, and a thick coating remains round each seed. The "gluten has been changed by digestion, and is much more sticky than when "in its natural state. After the rain has washed away the protecting layer of "skins, it washes the seeds off the bough in a curious way. The seeds appear "as if threaded on a fine white thread at about ¾ inch apart, and these threads "of seeds hang from the tree in lengths of from 12 to 18 inches. The wind "blows them about, and the free ends very quickly catch up on to some other "part of the tree, the gluten on the seeds holding them in place. I saw "festoons of these seeds everywhere. There had been a fairly heavy rain "the night before, but the wind blew the dangling threads in all directions." She states that the gluten in digested seeds remains soft and sticky for two or three days, and it may be longer, but that undigested gluten dries up by next day. The covering of skins is evidently intended to preserve the moisture until the rain comes and helps in the distribution.

The fullest account of the thrushes and mistletoe is given by Tubeuf (in his Monographie der Mistel, 1923) and Kronfeld ("Zur Biologie der Mistel," *Biol. Centralblatt*, 1888), and Coaz (in "Die Mistel in der Schweiz") gives a long list of other mistletoe berry-eating birds, but does not show that he has real evidence of their acting as dispersers. Among them he cites the Great Tit (*Parus major*), which, as I have mentioned, refused to take the berry when it found what it was. Plateau also gives a list of birds reported to eat the berries —fieldfare, blackbird, oriole, ringdove and jackdaw—but he is dubious about them all. The missel-thrush he thinks is the only dispersal agent, and attributes the absence of the plant in many places on the Continent to the absence of the thrush. Aigret's statement that rooks spread it by the adhesion of the viscid berries to their feet and feathers I have already mentioned under the account of rooks (*see* p. 453). I have never seen myself any other birds but missel-thrushes eat these berries, and I doubt if any other birds, except the song-thrush, do, nor have I seen any reliable account of any other disseminators. I have therefore omitted lists of birds like those of Coaz, which seem to consist merely of frugivorous and other birds and mammals, which the author thinks might possibly act as dispersal agents of mistletoe.

M. musicus, Song-Thrush.—This is a resident in England, but travels much about the country in small flocks. It eats perhaps fewer berries and drupes than the blackbird, as it prefers worms and snails when it can get them, but in the autumn and winter consumes a great quantity of fruits. I have seen it eating fruits of Hawthorn, *Euonymus oxyphyllus* and *E. europaeus*, *Ilex aquifolium* and *I. verticillata*, *Pyrus aria* and *Celtis occidentalis*, *Vitis Coignetiae* and *Solanum dulcamara*.

C. H. Hooper records its feeding on strawberries, gooseberries, and red currants, and "J. C." (in *Nature*) states that it eats the red drupes of *Daphne mezereon*. Mr. Dymes tells me he has once seen it eating the fruits of *Arum maculatum*. Campagna says it eats olives, in Italy. Pistone says in Sicily it feeds on the fruits of *Vaccinium myrtillus*, *Viburnum tinus*, *Myrtus communis* and *Rubi*. Holmboe records its feeding on the berries of *Vaccinium vitis-idea*, in Sweden. Sturm found it would eat those of *Adoxa moschatellina*, and Tubeuf

affirms that it eats Mistletoe berries, *Viscum album*, *V. cruciatum* and *Loranthus europaeus*, and Piccone adds *Hedera helix*, *Arbutus unedo*, *Olea europaea* and *Phytolacca decandra*. In Cornwall, Mrs. Rogers writes of the occurrence of *Griselinea littoralis* as an epiphyte in Pine trees probably dispersed by thrushes (*see under* Epiphytes, p. 30).

In New Zealand this bird, like the blackbird, was introduced and proved an important plant disperser. In the town belt of Dunedin, according to Thomson, when the area was protected from cattle, there was a marked increase in the plants *Fuchsia excorticata*, *Coprosma* spp., *Melicyrtus ramiflorus*, *Muhlenbeckia australis*, *Loranthus micranthus*, *Tupeia antarctica*; and gooseberries, currants, raspberries, *Leycesteria formosa* and *Sambucus*, as well as blackberries, were spread among the native vegetation by the thrush, aided by the blackbird.

Merula vulgaris, the Blackbird, is a most voracious eater of berries and drupes. If fruit is abundant on the tree on which it is feeding, after swallowing a large quantity of berries it flies to a distance and disgorges the seeds. If there is comparatively little fruit, it swallows and passes the seed. I have frequently found holly seeds and those of *Cotoneaster frigida* in the droppings. It eats largely of Holly, *Ilex aquifolium*, and *I. verticillata*, the Winter-berry of North America. Halfway through the month of November some bushes of the latter at Kew bore a great quantity of red berries, very conspicuous, as the plant is leafless then; by December 2nd all were gone, only some of the skins remaining. The berries are much more juicy than those of the European Holly, and were evidently more popular with birds than the drier and more pithy ones of the latter, and thus disappear much more readily. The song-thrush and bullfinch, however, eat a great quantity of them also.

In the same way the sweet juicy berries of the mountain ash, or Rowan tree (*Pyrus aucuparia*), are cleared off a tree in my garden within a few days of their being ripe, while those of *Pyracantha coccinea*, which actually touches the tree, and ripens its showy fruit a fortnight later, though sometimes attacked in September, is often not cleared of fruit till the middle of winter. Blackbirds feed on most species of *Cotoneaster*, temperate Asiatic trees, for the most part, which are often cultivated in our shrubberies. Now, I observed, among the collection of these shrubs and trees in Kew Gardens, that the inconspicuous black fruits of *Cotoneaster Wallichii*, which are remarkably sweet, were more sought after than the firmer red-berried kinds, nor did the blackbirds seem to care for the smaller black fruits of *C. bacillaris*, which were greedily devoured by greenfinches. They seemed to prefer the juicy fruits, especially during hot and dry weather, to the drier and more pithy kinds, possibly as a source of water-supply. Indeed, during some dry days in 1925 they began feeding on the Rowan tree berries actually before they were ripe. It is probable that this desire for liquid refreshment on dry days is the reason why many insectivorous birds, which do not drink water on the ground, attack juicy fruits like currants and cherries, just as the birds of all kinds in the Arizona deserts attack and devour the *Cactus* fruits. In Kew Gardens was a fine plant of *Vitis Coignetiae*, of Japan, climbing on an oak. This bore in September short racemes of sweet black grapes as big as large peas, densely crowded together. This vine was swarming with birds; blackbirds, thrushes, starlings and jays were devouring the juicy fruits, which were by no means conspicuous, being hidden among the splendid orange and red leaves.

Of *Pyracantha coccinea*, blackbirds eat the fruit very largely, at intervals, swallowing as many as from 17 to 30 in succession, after which they fly off and disgorge the seeds, presently coming back for another lot. In my garden they flew only a few yards to a plane tree, where they disgorged the seeds. Popular as this fruit is with birds, I have never seen seedlings coming up anywhere. In Kew Gardens and elsewhere I have seen the blackbird feeding

on the haws of *Rosa setistipula*, and fruits of *Pyrus baccata*, *P. sorbus*, *P. floribundus*, *P. aucuparia*, *P. Mougeotii*, *Hedera helix*, *Celtis occidentalis*, *Cornus macrophylla*, *Cotoneaster frigida*, *Morus alba*, *Euonymus europaeus*, *Symphoricarpus racemosus* and many *Crataegi*. Besides the fruits mentioned above, I have seen one pick up and carry off an acorn of *Quercus cerris*. Of *Symphoricarpus racemosus*, the Snowberry, I have seen them eating out the pulp and seeds, and leaving the skin. They do not seem to be as fond of this fruit as the American birds are, but eat it after other fruits are gone. I have only once seen a seedling bird-sown in Kew Gardens or elsewhere. They eat also the fruit of all species of *Crataegus*, wild or cultivated. I have seen them devouring the haws of *C. oxyacantha* and *C. coccinea* and *C. infera* of North America. The fruits of *C. coccinea* are bright red and as large as a small cherry. The leaves, which turn bright red in the autumn, sometimes fall off before the fruit is fully ripe, so that the tree in November is brilliant with the berries, and is cleared by the blackbirds in two or three days. There are often five or six birds in the tree at once. They pick up the fallen fruit as well as take them from the branches, and, when disturbed, fly off to some distance to eat them. Occasionally the tree retains its leaves till the fruit is ripe, but the birds still feed on the fruits.

Woodruffe-Peacock (*Selborne Mag.*, xxviii, 80) records these birds as sowing the seeds of *Daphne Laureola*, a shrub with black drupes, *Mahonia aquifolia* (of which blue fruit these birds are so fond that they carry it off directly it is ripe, and I have found seedlings at a considerable distance from the parent plant in the shrubberies, and under trees where the birds must have evacuated seeds), *Prunus pinnatifida* and *P. avium*, and he notes that they sowed gooseberries and red currants freely, black currants more rarely, and yellow currants not for many years, and he suggests that the birds thought that the yellow currants were unripe. All these plants, as well as raspberries, he found growing in pollard willows near his house. The same observer (in " A Fox Covert ") adds to the list of their food, fruits of *Bryonia dioica*, *Tamus communis*, *Lonicera caprifolium* and *Rhamnus catharticus*. E. M. Langley (*Nature*, lviii, 1898, 597) says that the blackbird eats, also, fruits of *Daphne mezereum*. Newstead adds to the list of food already given, strawberries and loganberries, but says it does not eat Mulberries (*Morus nigra*). I have, however, seen them greedily devouring the inconspicuous white fruit of *M. alba* in Kew Gardens.

Campagna says in Italy it feeds on *Fragaria vesca*, *Myrtus communis*, *Rubus discolor*, *Viburnum Tinus*, *Celtis australis*, *Coriaria myrtifolia*, *Daphne Gnidium*, *Vitis vinifera*, and Pistone adds to these *Vaccinium myrtillus*; Piccone, in Liguria, gives *Prunus avium*, *Arbutus unedo*, *Phytolacca decandra*, *Morus alba*, and *Juniperus communis* and *J. nana*. Tubeuf states that it eats the berries of *Viscum album*, and includes it with other thrushes as a feeder on *V. cruciatum* and *Loranthus europaeus*.

In New Zealand, where it has been introduced, according to Thompson (in his " Naturalisation of Plants in New Zealand," p. 419) it devours the fruit of *Leycesteria formosa*, a shrub introduced from the Himalayas, and *Loranthus Colensoi*, which parasite it spreads among the Hawthorn trees.

The bird is found in the Azores, and was perhaps the introducer, or at least is the disseminator, of *Ilex Perado*, *Prunus lusitanica*, *Fragaris vesca*, *Hedera canariensis*, *Myrica Faya*, *Juniperus*, *Ruscus aculeatus*, *Smilax canariensis* and *Arum italicum*; but the wood-pigeon is also an inhabitant of these islands, and may be responsible for some of these plants. The blackbird ranges from Europe to Persia and Turkestan.

Prof. Allman (in *Journ. Linn. Soc.*, xvii, p. 157) gives an account of the probable migration of *Pinguicula grandiflora* through the agency of birds. He states that he planted some specimens of *Pinguicula grandiflora*, from Cork, round a small pond at Parkstone in Dorest. They throve, but towards the

end of autumn he found they began to disappear, and before winter had well advanced, a large portion had vanished. He found that he often startled a blackbird or thrush from the neighbourhood of the marsh plants, and observed recent marks of beaks in the peat, and sometimes a recently eradicated *Pinguicula* could be seen lying on the ground. It was chiefly after the plants had passed into the bulb-like buds in which they continue during the winter, that they become liable to attack. He found later that at a distance of nearly 100 yards from the pond a healthy plant of the *Pinguicula*, with numerous vigorous flower stalks, had appeared. There was no possibility of the plant having been accidentally dropped there, and the only possible conclusion was that it was carried by a bird, and probably a blackbird.

Merula pilaris, the Fieldfare, is an Arctic bird which comes south in winter in large flocks, and is said to go as far as Asia Minor. It eats the berries of juniper, hawthorn, hips of roses, and fruit of Rowan tree and ivy (J. E. Harting, *Science Gossip*, 1870, p. 14). Miss A. H. Ware (*Essex Naturalist*, xx, 142) in "Gizzard Contents of Birds Collected by Miller Christie," records finding 10 hawthorn seeds in the gizzard of a fieldfare. Birger, in Sweden, found it feeding on *Empetrum nigrum*, and Tubeuf states it eats mistletoe berries. Pistone says in Sicily it feeds on *Vaccinium myrtillus*, *Viburnum Tinus*, *Myrtus communis* and *Rubi*. Piccone adds to these, *Arbutus unedo* and *Olea europaea*, and Heinitz gives *Hippophae rhamnoides* and *Prunus spinosa*. (I have very few records of any other birds eating the sea-buckthorn berries or sloes.)

Merula iliaca, the Redwing, is also an Arctic bird which migrates south in winter in small flocks, like the fieldfare. It feeds on berries of hawthorn and holly, and I have seen it eating the Siberian Crab (*Pyrus baccata*) in Kew Gardens (1926). Tubeuf states that it eats mistletoe berries, and Pistone adds *Vaccinium myrtillus*, *Viburnum Tinus*, *Myrtus communis* and *Rubi* to the list of its food-plants.

Merula torquata, Ring-Ousel, is a mountain bird inhabiting our moorlands, and migrating south during the winter to Italy and Africa. It feeds on Rowan tree, juniper and hawthorn berries and grapes. White ("Natural History of Selborne," letter xx) says it also eats ivy berries and yew fruit. Tubeuf says it feeds on mistletoe berries, and Pistone, in Italy, adds the fruit of *Vaccinium myrtillus*, *Viburnum Tinus*, *Myrtus communis* and *Rubi*. It probably feeds on the *Vaccinum* fruits on the Scotch moors also. Piccone adds the fruit of *Arbutus unedo*.

Merula Graysoni, a Mexican Thrush.—Nelson writes ("Birds of the Tres Marias Islands, Mexico"): "At the time of our visit a species of wild fig "was in fruit, and the tops of the trees were swarming with these robins (an "American word meaning thrushes) and other birds."

Merula simillima, Nilghiri Blackbird.—This Indian bird eats a good deal of fruit, especially of *Physalis peruviana* (Jerdon).

Turdus (*Pandestis*) *migratorius*, the American Robin, is largely a fruit-eater, and F. E. D. Beal (in *U.S.A. Agri. Bull.* 171, on "Food of Robins and Bluebirds") gives a very long list of fruits eaten by it, among which are :—*Juniperus monosperma*, *J. virginiana* and *J. communis*, *Sabal serrulata* (*Palmaceae*), *Smilax herbacea*, *S. bona-nox*, *S. glauca* (*Liliaceae*), *Myrica carolinensis*, *Ficus* sp., *Celtis occidentalis*, *C. mississipiensis*, *Morus nigra* and *M. alba* (Hart-Merriam), *Phoradendron californicum*, *Rumex* sp., *Polygonum persicaria*, *Phytolacca decandra*, *Persea borbonia*, *Lindera benzoin* and *Sassafras officinalis* (*Lauraceae*), *Pyrus malus*, *P. diversifolius*, *P. americanus*, *Prunus domestica*, *P. virginiana*, *P. cerasus*, *P. pennsylvanica*, *Amelanchier florida*, *A. alnifolia*, *A. canadensis*, *Crataegus oxyacantha*, *Fragaria*, *Rubus* sp., *Melia azederach*, *Oxalis* sp., *Alsine* sp., *Rhus typhina*, *R. glabra*, *R. copallina*, *R. radicans*, *Schinus molle*, *Ilex opaca*, *I. decidua*, *I. verticillata*, *Euonymus*

americanus, *Celastrus scandens*, *Berchemia volubilis*, *Rhamnus Purshiana*, *Parthenocissus quinquefolia*, *Vitis Labrusca*, *V. aestivalis*, *V. cordifolia*, *V. californica*, *Cornus florida*, *C. asperifolia*, *C. paniculata*, *C. alternifolia*, *Nyssa sylvatica*, *N. aquatica*, *Gaylussaccia*, *Vaccinium oxycoccus*, *Diospyros virginianus*, *Olea europaea*, *Diodia teres*, *Lonicera japonica*, *Symphoricarpus racemosus*, *Viburnum dentatum*, *V. prunifolium*, *Sambucus canadensis* and *S. pubens*, *Ambrosia artemisaefolia* and *Berberis vulgaris*. This bird, in the abundance and variety of its food-plants, seems to take the place of our blackbirds, in America.

Turdus mustelinus, an American bird, eats fruits of *Morus nigra* and *M. rubra* (Hart-Merriam).

Turdus javanicus var. *fumida* eats the fruit of *Vaccinium waringiaefolium* on the volcanic mountains of Java (Van Leeuwen).

T. hoemorrhous, a Javanese Thrush.—Valeton (in his "Distribution of Fruits by Animals in Java") states that this bird disseminates the seed of *Lantana mixta* (*L. camara*).

T. magellanicus.—This Thrush is, according to C. Skottsberg, the only fruit-eater in Juan Fernandez ("Natural History of Juan Fernandez," ii, 1928), though, as he points out, there are 29 eatable fruits on the islands. Of these, *Juania*, *Ugni*, *Myrceugenia*, *Pernettya*, *Rubus*, *Empetrum*, *Myrteola*, *Gunnera* and *Nertera* have red or orange fruits; *Drimys*, *Azara*, *Coprosma*, *Santalum*, *Phrygilanthus*, *Aristotelia*, black; *Berberis*, *Solanum*, *Raphithamnus* and *Cuminia*, black or violet; *Griegia margyricarpus*, *Ochagavia*. whitish. He notes that *Aristotelia* has only within the last 10 years been found in Masafuera. The thrush migrates from one island to the other, and probably carried the seed.

Cochroa azurea.—Koorders found the crop of this bird, in Java, full of seeds of a rutaceous shrub, probably *Fagara* (*Zanthoxylum*) *scandens*, which was common in the neighbourhood. *C. purpurea* of India feeds largely on stony berries (Jerdon).

Phaeornis sp.—According to Perkins, this endemic bird of the Hawaiian Islands eats the fruits of *Osmanthus* (*Oleaceae*), *Straussia* (*Rubiaceae*), *Cheirodendron* (*Araliaceae*), and also the red drupes of *Wikstroemia foetida* (*Thymeleaceae*).

Hylocichla ustulata, the Russet-Backed Thrush of California, eats the fruit of *Rubi*, *Sambucus*, *Lonicera involucrata*, *Schinus molle*, *Solanum* sp., *Rhamnus californicus* and *Rhus diversiloba* (Beal, *U.S.A. Dept. Agric. Bull.* 30, 1907); and *H. guttata* eats the fruit of the *Schinus* and *Rhus*, and Mistletoe berries (*Phoradendron*).

Geocichla Wardii, the Pied Ground-Thrush of Ceylon, feeds on Guavas and figs; and *Oreocinchla aurea* var. *Horsfieldii*, of Java, according to Van Leeuwen, was found eating the berries of *Myrica javanica* on Mount Papandayan.

Monticola cyanus, Blue Rock-Thrush, a South American bird.—Campagna (in "Richerche sulla Disseminazione per Ucelli carpofagi, Malpighia," xxi, 1907, p. 523) states that in Italy this thrush eats the fruit of *Crataegus oxyacantha*, *Ficus carica*, *Viburnum tinus*, *Daphne gnidium*, *Vitis vinifera*, *Phytolacca decandra*, and *Myrtus communis*, and Piccone says that *M. saxatilis* eats the fruit of *Morus alba*.

Accentor modularis, the Hedge Sparrow, is chiefly insectivorous, but Holmboe has recorded it as eating the fruits of the Nettle (*Urtica dioica*) and Raspberry (*Rubus idaeus* and *Sambucus racemosus*). Piccone records it as eating *Arbutus unedo*, as does the Alpine accentor, *A. alpinus*.

Nesocichla crenata, the Tristan d'Acunha Thrush.—This thrush is peculiar to the island of Tristan d'Acunha, where Moseley (in "Notes of a Naturalist," p. 122) says: "The thrush *Nesocichla crenata* feeds on the berries of the little *Nertera*."

Nicol (in " Three Voyages of a Naturalist ") says : " The Steward bought " from the natives of Tristan d'Acunha a quantity of small berries, which, " when stewed, were much like cranberries in flavour. This fruit, which we " were told was the principal food of the thrush-like bird, is probably *Nertera* " *depressa* mentioned by Moseley " (but it is more probable that it was *Empetrum rubrum*).

Ixoreus naevius, Varied Thrush, Oregon Robin, an American bird extending along the north-west coast of California to Alaska. According to Beal (*U.S.A. Agric. Bull.* 171), it feeds on Juniper, apple, *Rubus*, *Erodium*, *Schinus molle*, *Rhus diversiloba*, *Rhamnus*, *Solanum nigrum*, *Lonicera californica*, *Symphoricarpus rotundifolius* and *S. racemosus*.

Sialis sialis, the American Blue-bird, feeds, according to Beal, on the berries of *Juniperus virginianus* and grains of some grasses, *Panicum* sp., *Setaria* sp., and wheat ; also the fruit of *Asparagus officinalis*, *Smilacina racemosa*, *Smilax bona-nox*, *S. rotundifolia*, *Myrica carolinensis*, *Celtis occidentalis* and *mississipiensis*, *Morus nigra* and *M. alba* (Hart-Merriam), *Phoradendron flavescens*, *Rumex*, *Polygonum*, *Amaranthus*, *Phytolacca decandra*, *Persea borbonia*, *Ribes*, *Crataegus*, *Rubus*, *Rosa*, *Prunus serotina* and *P. virginiana*, and *V. pennsylvanica*, *Rhus typhina*, R. *glabra*, R. *copallina*, R. *vernix*, R. *radicans*, and R. *venenata* (Barrow states that he found large numbers of seeds of this poison Sumach in the stomach of the blue-bird), *Ilex cassine*, *I. decidua*, *I. verticillata* and *I. glabra*, *Euonymus americanus*, *Celastrus scandens*, *Condalia* sp. (*Rhamneae*), *Parthenocissus quinquefolia*, *Aralia* sp., *Cornus florida*, *C. asperifolia*, *C. alternifolia*, *Nyssa sylvatica* (Barrow states that the little bird swallows whole the large fruits of Sour Gum, *Nyssa* and *Cornus florida*), *Gaylussacia*, *Schinus molle*, *Vaccinium*, *Diospyros virginianus*, *Solanum* sp., *Diodia teres*, *Mitchella repens*, *Viburnum opulus*, *Sambucus canadensis* and *Ambrosia*.

Sialis mexicana, the Western Blue-bird, feeds on *Sambucus*, *Phoradendron californicum*—which is popular with it—*Rumex*, *Polygonum*, *Amelanchier alnifolia*, *Rubi*, *Pruni*, *Vitis*, *Rhus copallina* and R. *diversiloba*, *Schinus molle*, *Solanum* and *Ficus*.

Sialis currucoides, the Mountain Blue-bird, which inhabits high altitudes in North America, eats the fruits of *Ribes*, *Sambucus*, *Vitis* and *Rhus*.

Saxicola oenanthe, the Wheatear, feeds almost exclusively on insects, but Holmboe found it eating Rowan tree berries in Scandinavia.

Erithacus cyanaeculus. — Sturm says it will eat the berries of *Adoxa moschatellina*.

Philomela luscinia, the Nightingale, according to Piccone, eats strawberries and red currants in Liguria.

Ruticilla rubecula, the Robin, feeds mainly on insects, but also takes a certain quantity of fruit. Meyer records its feeding on Elderberries (*Sambucus*) and blackberries. Oldham (in " Witherby's Practical Handbook of British Birds," p. 483), says that the remains of raspberries and currants were found in pellets ejected by robins. Holmboe adds Rowan tree berries. It also eats ivy berries, and, according to Hooper, strawberries, cherries, and grapes. Harting says it is very fond of the berries of *Solanum dulcamara*. Sturm found it would eat those of *Adoxa moschatellina*. I have seen it take the arillate seed of *Euonymus europaeus*. Tubeuf says it eats mistletoe berries, and Piccone the fruits of *Rubus discolor*, *Arbutus unedo*, and *Phytolacca decandra*.

R. *phoenicurus*, the Redstart.—H. Collett (in " Holmboe's Account of Bird Food in Scandinavia ") states that he found 56 seeds of *Cornus alba* in a nest of this bird, which were taken from a bush hard by, and Piccone says it eats also the fruit of *Arbutus unedo*, as does also the Black Redstart (R. *tithys*).

REGULIDAE.—Goldcrests.

Regulus calendula, North American Ruby-crest or Kinglet, eats Elderberries (*Sambucus*) (Beal); and *R. ignicapillus* and *R. cristatus*, according to Piccone, feed, occasionally at least, on juniper berries in Italy.

TROGLODYTIDAE.

Anorthura troglodytes, the Wren.—Usually an insect-eater. Sturm says it ate fruits of *Adoxa moschatellina*.

MIMIDAE.

According to Toumey, the fruit of the giant Cactus (*Cereus gigantea*) is attractive to many birds in the Arizona deserts, and nearly a hundred different kinds feed on it. Among them he mentions the Thrashers (*Mimidae*).

Mima polyglottis, the Mocking-bird of North America, feeds largely on fruits, eating those of the Poison Ivy (*Rhus radicans*) (Henderson), Poison Oak (*Rhus diversiloba*), *Sambucus*, *Rubi*, grapes and figs (Beal), *Juniperus virginianus* (Phillips), *Phytolacca decandra*, *Diospyros* (Persimmons, both wild and cultivated kinds), *Duranta Plumieri*, *Melia azederach* and *Yucca aloifolia*, and other species (Webber). The latter author gives accounts of the dispersal of *Yucca* seeds by this bird in the *American Naturalist*, and in the Reports of the Missouri Botanic Gardens. The fruit of the section *Sarco-yucca*, *Y. baccata*, etc., have sweet edible fruits. The mocking-bird eats the pulp of the fruits, but does not usually swallow the seeds, though it occasionally does so accidentally. The seeds, sticky with the pulp, adhere to the bill of the bird, and are jerked off by it to a distance of 3 to 6 feet (1 to 2 metres). The *Yucca* fruits fall of themselves, when ripe, and are carried off by small mammals, and the seeds in the dehiscent capsular species fall off and, striking the reflexed leaves, bound away.

He says that the *Yucca* moth larva also sometimes bites off the whole bunch of fruit, and it falls or rolls away. But it is obvious that the most important means of dissemination he mentions is the swallowing of the seed by the bird.

Galeoscoptes carolinianus, the Cat-bird of North America, eats Mulberries (*Morus niger* and *M. alba*) (Hart-Merriam).

Cichlhermina fuscata, of St. Croix, according to Newton, feeds on guavas and mangoes.

CINCLIDAE.

The Dippers (*Cinclus aquaticus*) live mainly on aquatic insects and molluscs, but Holmboe records finding one with its stomach full of the fruits of *Alisma plantago*.

TIMELIDAE—Babblers.

These tropical Old World birds feed largely on insects and weed-seeds, but some eat fleshy fruits.

Mixornis ruficapilla feeds on the small fruits of *Laportea stimulans* (*Urticaceae*) in Sumatra (Jacobson). These fruits are small, white or pink fleshy achenes, eaten by several kinds of birds. There are 2 species of *Laportea* in Christmas Island.

Alcippe solitaria, according to Koorders, eats fruits of *Araliaceae* (probably *Schefflera* sp.) in Java.

Samuela cinnamomea.—In the stomach of this Australian bird A. M. Lea found seeds of *Portulaca oleracea*, *Hibiscus* sp., *Setaria viridis* and *Erodium cygnorum*.

Melanocichla lugubris, the Babbling-Thrush of the Malay Peninsula, eats raspberries (probably the fruit of *Rubus rosaefolius*), according to H. C. Robinson.

Trochalopterum cachinnans, the Nilghiri Laughing-Thrush, feeds chiefly on fruit, especially that of *Physalis peruviana* (Jerdon).

Crateropus canorus, Jungle Babbler of India, eats fruit of *Zizyphus jujuba*, and several species of *Ficus* (Mason).

CAMPOPHAGIDAE.—Cuckoo-Shrikes.

Coracina novae-Hollandiae.—This is recorded by A. M. Lea as feeding on *Loranthus exocarpi* in Australia.

PYCNONOTIDAE.—Bulbuls.

These little thrush-like birds are abundant in Africa, India, and Malaya, inhabiting open country generally, and feeding almost exclusively on fruits of small size, so that they are important plant-disseminators over large areas.

Otocompsa analis, the Yellow-vented Bulbul, is a very common Malayan bird, and a very active seed-disperser. In the Singapore Botanic Gardens it ate the fruits and disseminated the seeds of *Rhodamnia trinervia*, *Melastoma polyanthum*, *Clidemia hirta*, *Olea maritima*, *Wulfia stenoglossa*, *Ficus benjamina*, *Cinnamomum iners*, *Embelia garciniaefolia*, *Lantana mixta*, with black fruits, *Fagraea imperialis*, orange pulp, *Cyrtophyllum fragrans* and *Passiflora foetida*, with yellow or orange fruits, and the seeds of *Wormia suffruticosa* with its red arils, and many other small-sized fruits. The *Melastoma* is the first shrub to appear in the Lalang grass fields, where it is disseminated mainly by this bird. *Clidemia*, an introduced American plant, has been conveyed by it to several distant spots from the Botanic Gardens, whence it originated. *Passiflora foetida*, also an American plant, is widely disseminated by it. On the banks of the Tembeling River, in Pahang, I saw this plant on newly-cleared ground, accompanied by this bulbul, which is not a forest bird, and had evidently followed cultivation along the river, probably bringing the Passion-flower with it. *O. jocosa* also feeds largely on the fruits of *Lantana*, and H. C. Robinson has seen it feeding on the fruits of the wild Cashew Nut (*Anacardium occidentale*) in the Malay Peninsula. The fruits of this wild form are not too large for this bird to carry to some distance.

Chloropsis aurifrons.—This bulbul is said to be entirely insectivorous, but Stuart-Baker found numerous black seeds of a leguminous plant in two crops. The pods were crowded with tiny blue beetles, so that the bird may have swallowed the seeds accidentally with the beetles, and, as mentioned before, Keeble found the crop of *Chl. Jerdoni* containing fruits of *Loranthus*.

Pycnonotus plumosus, in the Malay Peninsula, feeds largely on the blue "berries" (seeds) of a species of *Sterculia* (Robinson). I believe it was *Otocompsa* which persistently carried off the seeds of *Sterculia Jackiana* close to my house in Singapore, but never saw them at it. The seeds are unusually large for so small a bird to swallow. Guppy seems to have been doubtful as to how the *Sterculias* were imported into the Polynesian Islands, but it was undoubtedly by birds. The pulp on the seed is so thin that one would hardly think it worth while for a bird to swallow so large a seed.

P. aurigaster, of Java, is stated by Van Leeuwen, on the authority of Van Welsem, to feed on the berries of *Phytolacca purpurascens* (probably *P. decandra*).

P. haemorrhoidalis in Java is known to eat the fruits of *Myrica javanica* (Vordermann).

P. brunneus, of Sumatra, feeds on the fruits of *Laportea stimulans* (*Urticaceae*), Jacobson (in "Birds of Korinchi," Robinson and Kloss, *Journ. F.M.S. Mus.*, xi, 202).

P. bimaculatus, a mountain bird of Sumatra and Java, eats the berries of *Vaccinium* sp., and the achenes of *Gahnia javanica* (*Cyperaceae*), according to Jacobson. This is a widely-distributed mountain sedge occurring in Sumatra, Java, and the Malay Peninsula. The achenes are yellow, and conspicuous against the black spike of inflorescence hanging out in the stamen filaments. The same bird eats the drupes of *Embelia ribes* (probably *E. garciniaefolia*, and the seeds of *Glochidion* sp. in Java (Koorders).

P. chryssorhoides, of China, Swinhoe ("Ibis," iii, 39) writes :—"I observed "numbers of these bulbuls feeding on the ripe fruit of the Tallow tree (*Stillingia* "*sebifera* (*Euphorbiaceae*) in company with *P. occipitalis*."

Criniger flaveolus.—Stuart-Baker says that he took from the stomach of this bird 2 fruits of *Phyllanthus Emblica*. This fruit is round, green and about 1 inch through, very large for a small bird like this to swallow.

Rubigala squamata and R. *Webberi*, in Sumatra, are very fond of figs, and R. *dispar* of the fruits of *Laportea stimulans* (Jacobson); *Brachypodeus* sp. is also a fig-eater.

Molpastes hoemorrhous, the Red-vented Bulbul, feeds on the fruits of *Physalis peruviana* and on raspberries; *M. burmanicum* also on raspberries; *M. bengalensis* on Pomegranates (*Punica Granatum*), *Zizyphus jujuba*, figs of *Ficus religiosa* and Loquats, *Eriobotrya japonica* (Mason).

M. intermedius.—R. W. C. Hingston (in "A Naturalist in Himalaya," p. 260) writes of this bulbul: "The birds used to congregate in winter on the "branches of the Persian lilac (*Melia Azederach*) to feed on its nutritious "berries. They usually pinch these berries to pieces; they will hammer them "to fragments like a nuthatch, and even at times swallow them whole. Now, "these berries are from 1½ to 2 inches in circumference, an enormous bulk "for these little birds to swallow, yet these bulbuls, after strenuous efforts, "succeed in getting the whole berry down along the gullet. The circum-"ference of the bulbul's empty gullet is only ½ inch, and the circumference "of the whole neck 1[1] inches, so it is clear that this bulbul is in the habit of "swallowing objects not only 3 times the dimensions of its own gullet, but "even wider than its own neck. It is, of course, the highly distensible nature "of the soft parts that permits the passage of such large mouthfuls. Anything "that passes the gape can with ease continue down the gullet." *Melia Azederach*, introduced into Christmas Island, was widely dispersed all over the area near the settlement, evidently by birds, probably *Merula erythropleura*, the local thrush, as the fruits would be too large for the *Zosterops*, though the bat *Pteropus* may have helped.

HIRUNDINIDAE.

The swallows and martins seem the most unlikely of all birds to eat fruits, but such a fact is recorded. W. S. Barrows (in "Seed-planting by Birds," *U.S.A. Dept. Agric. Report*, 1890, p. 280) writes :—"Fishermen and farmers "along the Atlantic coasts (of North America) state that swallows ate the fruits "of the Waxberry or Bayberry (*Myrica cerifera*) in thousands before starting "for the south in August. It is certain that the White-bellied Swallow "(perhaps *Tachycineta bicolor*), the Bank Swallow (*Cotile riparia*), the Barn "Swallow (*Hirundo erythrogastra*), and the Tree Swallow (*Dendroprocne bicolor*) "eat bayberries to a large extent." It seems extraordinary that the Bank Swallow, our Sand-Martin, should eat fruit in America.

MUSCICAPIDAE.—FLYCATCHERS.

Most of these are strictly entomophagous, but a few take fruits.

Poliomyas luteola, according to Koorders, feeds on *Glochidion* and the drupes of *Embelia ribes* (probably *E. garciniaefolia*) in Java.

Niltava grandis has been seen eating raspberries (*Rubus rosaefolius*) in Sakai clearings, and the fruit of *Lantana* in Thaiping, Perak, in the Malay Peninsula, by Robinson.

Siva strigula, on the mountains of the Malay Peninsula, eats the fruits of *Baeckia frutescens* (*Myrtaceae*), according to Robinson, and may be the disseminator of this far-spread plant.

TYRANNIDAE.

The Tyrant birds are usually considered insect-eaters only, but the American ornithologists have shown that they do eat fruit also. They are peculiar to North and South America, and take the place of the Flycatchers of the Old World.

Barrows says that, having seen a King-bird (*Tyrannus*) gorging itself with cherries, his faith in purely insectivorous birds was considerably shaken. Hart-Merriam says that *Tyrannus tyrannus* feeds on Mulberries (*Morus nigra* and *M. alba*), and Phillips states that it eats also berries of *Juniperus virginianus* and *J. sabina*. Beal (in the *U.S.A. Agri. Bull.*, 1912, p. 44, on the "Food of Our More Important Flycatchers") adds, as the food of this bird, *Taraxacum dens-leonis*, *Sambucus canadensis*, *Solanum nigrum*, *Vaccinium* sp., *Gaylussacia*, *Cornus alternifolia*, *C. paniculata*, *C. asperifolia* and *C. amomum*, *Vitis vulpina*, *V. cordifolia*, *V. labrusca*, *Ampelopsis quinquefolia* (Virginia creeper), *Condalia obovata*, *Rhamnus lanceolatus*, *Prunus cerasus*, *P. pennsylvanica*, *P. virginiana*, *P. serotina*, *Rubi*, *Fragaria vesca*, *Amelanchier*, *Pyrus arbutifolius*, *Ribes*, *Lindera Benzoin*, *Sassafras officinalis*, *Phytolacca decandra*, *Amaranthus* sp., *Myrica carolinensis*, *Rhynchospora* and *Setaria*.

Tyrannus caudifasciatus and *T. cristatus* feed on the large red berries of the Tropic Birch (*Bursera gummifera*) in Jamaica (Gosse).

T. verticalis eats the fruits of the Virginia creeper, *Crataegi*, *Sambucus*, and olives, according to Beal.

Myriarchus crinitus feeds on mulberries and fruit of *Phytolacca*, *Sassafras*, *Lindera Benzoin*, *Pruni*, *Vitis*, *Cornus* and *Sambucus*; and *M. cinerascens* on those of *Solanum nigrum* as well.

Sayornis Phoebe feeds on *Juniperus virginianus*, *Smilax Bona-nox*, *Myrica carolinensis* and *M. cerifera*, *Celtis mississippiensis* and *C. occidentalis*, *Polygonum*, *Phytolacca*, *Cocculus carolinus*, *Lindera Benzoin*, *Sassafras*, *Amelanchier*, *Pruni*, *Cassia* sp., *Rhus copallina*, R. *glabra*, R. *vernix*, R. *toxicodendron*, *Ilex cassine*, *Cissus*, *Cornus*, *Diospyros virginiana*, *Symplocos tinctoria*, *Sambucus*, and *Ambrosia*. *S. Sayus* has been found to eat fruit of *Sambucus glaucus*, *Madia sativa*, and *Solanum nigrum*. *S. nigricans* feeds on *Sambucus glaucus*, *Cornus pubescens*, *Erodium* sp., *Rubi* and *Rhus* fruits.

Myriochanes virens and *Empidonax* eat much the same fruit, while *Empidonax minimus* eats also fruit of *Oxalis stricta*.

Myiadestes (*Muscicapa*) *armillaris*, the Solitaire Bird of Jamaica, eats fruits of a species of *Rubus*, of a Mistletoe (either *Loranthus* or *Phoradendron*), "glass-eye berries," and Pimento (Gosse).

EURYLAEMIDAE.—BROADBILLS.

These birds inhabit the forests of tropical Asia and feed mostly on insects. However, *Calyptomena viridis*, a common bird in the forests of the Malay

Peninsula and Sumatra, is a fruit-eater—in fact, Mason says in India it feeds entirely on fruit. *Cymborrhynchus macrorhynchus*, and *Serilophus lunatus* of India are reported to feed sometimes on berries.

COTINGIDAE.

Tityra leuconotis, the Black Shrike of Jamaica, feeds on the large berries of *Bursera gummifera* (Gosse).

The section *PIPRIDAE* (manakins) are South American fruit-eaters, but I have no records of the fruit eaten by any of them.

PICIDAE.—Woodpeckers.

The Woodpeckers of Europe seem to feed entirely on insects, but in America they by no means confine themselves to this food, and many species eat a considerable quantity of fruit.

Toumey states that in the Arizona deserts the wood-peckers eat the fruit of *Cereus giganteus*. It seems probable that they attack these juicy fruits for the sake of the water in them. Beal (in "Food of Woodpeckers," *U.S.A. Dept. Agri. Biol. Survey*, 1911, *Bull.* 37) mentions the following species of American woodpeckers, with their fruit-food: *Dryobates villosus* eats fruit of *Myrica cerifera*, *Morus rubra*, *Sassafras*, *Lindera Benzoin*, *Amaranthus* sp., *Phytolacca decandra*, *Vaccinium* sp., *Sambucus*, *Nyssa*, *Cornus florida* and *C. asperifolia*, *Amelanchier canadensis*, and *A. alnifolia*, *Aronia* sp., *Fragaria* sp., *Prunus virginiana*, *P. serotina*, *Parthenocissus quinquefolia*, *Rhus glabra*, R. *vernix*, R. *radicans*, and seeds of *Magnolia foetida*.

Dryobates pubescens eats also fruits of *Pyrus (Sorbus) americanus* and *Cornus alternifolia*, and also mulberries (Hart-Merriam).

Centurus carolinus, the Red-bellied Woodpecker, eats, besides many of the above fruits, those of *Aralia nudicaulis*, *Opuntia* and *Ilex opaca*, and *I. rubra*.

Sphyrapicus varius is known to eat the fruits of *Juniperus virginianus*, *Smilax*, *Celtis occidentalis*, *Sassafras*, *Rubi*, *Amelanchier*, *Prunus virginiana* and *P. serotina*, *Rhus vernix* and R. *radicans*, *Ilex opaca*, *I. glabra*, *I. decidua*, *I. verticillata*, *Euonymus americanus* (seeds), *Vitis cordifolia*, *Parthenocissus quinquefolia*, *Cornus florida*, *Nyssa*, *Vaccinium*, *Solanum nigrum*, *Sambucus pubescens*, *Phytolacca decandra*. *Sphyrapicus ruber* eats, besides, fruits of *Schinus molle* and *Rhamnus californicus*.

Melanerpes erythrocephalus, the Red-headed Woodpecker, devours fruits of *Smilax bona-nox*, *Morus rubra*, *Chenopodium album*, *Amelanchier*, *Prunus pennsylvanica*, *P. virginiana* and *P. serotina*, *Rhus copallina*, R. *glabra* and R. *radicans*, *Vitis vulpina* and *V. cordifolia*, *Parthenocissus quinquefolia*, *Cornus florida*, C. *asperifolia* and C. *candidissima*, *Nyssa*, *Gaylussacia*, *Solanum nigrum*, *Sambucus canadensis* and *S. pubens*.

Colaptes auratus, the Flicker, eats berries of *Smilax glauca*, *S. rotundifolia*, *S. bona-nox*, *S. laurifolia*, *Comptonia (Myrica) peregrina*, *Polygonum lapathifolium*, *P. persicaria*, *P. convolvulus*, *Rubus cuneifolius*, *Prunus avium*, *Ilex cassine*, *Nyssa aquatica* (Beal), and *Rhus radicans* (Henderson).

Of the European Woodpeckers, *Picus leuconotus*, *Drycopus Martianus* and *Gecinus canus* are recorded by Holmboe as feeding on Rowan tree berries (*Pyrus aucuparia*) in Sweden. *Gecinus viridis*, the Green Woodpecker, is said by Pycraft to eat berries occasionally. Tubeuf says that some of the European woodpeckers eat mistletoe berries.

Centurus radiolatus, a Jamaican Woodpecker, feeds on Soursop (*Anona muricata*) and the fruits of *Cordia collococca* Sw., and the crimson berries of *Citharexylon*.

Iynx torquilla, the Wryneck, is usually an insect-eater, but Sturm states it ate berries of *Adoxa moschatellina*; and Meyer says that in autumn, when insects are scarce, it eats elderberries.

MUSOPHAGIDAE.—PLANTAIN-EATERS.

The Turacos of Africa feed largely on fruits, of what kind is seldom recorded. *Turacus corythaix* is recorded by Phillips as eating the fruits of *Ekebergia capensis* (*Meliaceae*), *Olea laurifolia* and *Curtisia faginea*, in Knysna, South Africa, and Burtt found fruit of *Grewia platyclada* in its crop when shot, and says that a long-tailed bird resembling a turaco was observed several times swallowing fruits of *Zizyphus mucronatus* and *Grewia fallax*.

CAPITONIDAE.—BARBETS.

The Barbets, forest birds of the tropics of Asia, Africa, and America, feed largely on fruits, and especially on figs, though also on insects. Beccari ("Nelle Foresti di Borneo") mentions buccos (i.e., barbets) as feeding on figs in Borneo, and C. H. T. Marshall (in his Monograph of Barbets) records the following as feeding on these fruits: *Pogonorhychus bucocephalus*, of Africa; *Megalaema corvina*, *M. armillaris* and *Xantholaema rosea*, of Java; *X. rubricapilla*, of Ceylon. *X. haematocephala*, of India, feeds specially on the figs of *Ficus retusa* and *F. Rumphii* (D. D. Cunningham).

Megalaema Hodgsoni, of the Himalayas, eats wild loquats (Marshall), and *M. armillaris*, of Java, coffee berries; *Barbatula pusilla*, of Africa, mulberries (Marshall). From the stomachs of *Cyanops armillaris*, of Java, Koorders obtained seed of an *Antidesma*, probably *A. tetrandrum* (*Euphorbiaceae*), and of a *Ficus*.

Thereiceyx zeylonicus, in India, feeds on figs of *Ficus bengalensis*, fruit of *Zizyphus jujuba* and Loquat (*Eriobotrya japonica*) (Mason); and Lewis says that Ceylon barbets feed on the fruits of *Zizyphus napeca*.

RHAMPHASTIDAE.

The Toucans of South America take the place of the hornbills of Asia, and feed as freely on fruits. W. H. Edwards (in "A Voyage of the River Amazon," 1847) writes of the Palm *Euterpe edulis*: "The fruits, at first green, "soon turn purple, and are fully ripe. Flocks of toucans, parrots and other "fruit-loving birds are first to discover them, but there are too many even "for the birds. The fruit is covered by a thick skin, beneath which, embedded "in a very slight pulp, is the stone. There are many varieties (of toucans), "but the Red-billed (*Rhamphastes erythrorhynchos*) and *Ariel* (R. *ariel*) are the "largest and most abundant. As far as we could observe, they merely threw "back the head, allowing the fruit to fall down the throat."

CUCULIDAE.—CUCKOOS.

Most of the Cuckoos feed mainly or entirely on insects; a few, however, are fruit-eaters. *Eudynamis orientalis*, the Asiatic Koel, is a fruit-eater. Vorderman records finding seed of figs (*Ficus*) in their crops in Java. Mason says it eats fruit of *Ficus bengalensis* and *F. religiosa*, mulberries, *Mimusops Elengi*, and *Nephelium Litchi*, disgorging the large seeds of these latter fruits.

Coccyzus americanus.—Henderson records this as feeding on poison-ivy fruits (*Rhus radicans*) in America, and Dr. C. Hart-Merriam states it feeds also on mulberries.

Crotophaga ani, Jamaica, feeds on the berries of *Citharexylon* and of Snake-withe (Gosse).

Centropus superciliosus.—H. O. Forbes (in the "Natural History of Socotra") records this as feeding on the fruits of *Zizyphus spina-christi.*

Hierococcyx varius, Hawk Cuckoo, is very fond of the fig of the Banyan (*Ficus bengalensis*), and other figs (Jerdon).

TROGONIDAE.

The Trogons are largely insectivorous, but Jacobson (*Journ. F.M.S. Mus.*, xi, 202) states that they eat some fruits also.

Vorderman found seeds of *Ficus* in the crops of trogons in Java, and Nelson records (in " Birds of the Tres Marias Islands, Mexico ") that *Trogon ambiguus* was swarming in the tops of the wild fig trees, with other birds, when the figs were ripe.

BUCEROTIDAE.

The Hornbills, though they eat lizards, rats, and other animal food, feed mainly on fruits of trees, and, owing to their large size, swallow very large fruits. They fly for long distances, and go from forest to forest in search of fruit. Some species occur in Africa, others in India, but they are most abundant in the Malay region. Some notes on the feeding of captive hornbills are to be found under the section dealing with the duration of time in which birds retain seeds before passing them (p. 448). They, next to the pigeons, are probably the widest dispersers of the Nutmegs (*Myristicaceae*), and they feed also largely on figs (Beccari, " Nelle Foreste di Borneo ").

Buceros ruficollis visits the nutmeg plantations of Ceram and devours the Nutmegs (*Myristica moschata*) and Canary Nuts (*Canarium*). It is said to fly from Papua (S. Muller, Reise II, 1856, 37, Temminck, " Coup d'Oeil," iii, 1849, p. 294).

Rhytidoceros obscurus.—Vorderman found fig seeds in the crops of this Javanese Hornbill.

Lophoceros melanoleucus, the African Hornbill, feeds on the fruits of *Ekebergia capensis* and *Olea laurifolia* in Knysna (Phillips). *L. birostris*, the Grey Hornbill of India, feeds almost exclusively on fruits, chiefly figs (*Ficus bengalensis*, *F. religiosa*, and others) (Mason).

Anthracoceros malabaricus and *A. convexus* are also especially fond of figs, *Kayu ara* (probably *Ficus retusa*) in the Malay Peninsula (Kloss, " Ibis," 1911, p. 36).

A. coronatus.—Gamble (" Manual of Indian Timbers," 498) says that the Malabar Hornbill eats the fruit of *Strychnos nux vomica*, but the seeds are always rejected and not digested. *A. albirostris*, of India, feeds on figs. *Rhinoplax vigil* is, according to H. C. Robinson, very fond of the green pods of *Parkia speciosa* (*Leguminosae*), which are very popular with natives, and which cause both man and bird to exhale a horrible odour. These pods are large and green, and borne on a lofty tree in the Malay Peninsula.

Troup mentions the fruit of *Diospyros melanoxylon* as a fruit eaten by Indian Hornbills, which birds may often be seen in quantities in the trees, and says they also feed on the fruits of *Bridelia retusa*, which are yellow-green at first, turning purplish black, and those of *Elaeodendron glaucum*, obovoid drupes which are eagerly sought by hornbills. Spittal (in " Wild Ceylon ") says that these birds feed on the milky yellow berries of *Mimusops hexandra* in Ceylon.

STEATORNITHIDAE.—OIL-BIRDS.

Steatornis caripensis, the Oil-bird or Guacharo, lives in deep caves at Caripe, Venezuela, and Trinidad, and feeds on oily fruits and seeds. It is nocturnal,

and flies far out into the woods to seek for these fruits, which it brings back to its caves for the young ones. It swallows the fruit of species of *Achras*, *Aiphanes*, *Laurus* and *Psychotria*. Johow ("Vegetation's bilder aus West Indien and Venezuela," *Kosmos*, 1885, ii, 199) says: "In the excreta were "found the seeds of *Psychotria arborea*" (a name I cannot trace anywhere else, but possibly *P. rufescens*, a tree-species growing at Caripe).

Funck (*Bull. Acad. Sc. Bruxelles*, xi, 2, 371) says he found in the cave, a seed of a tree which he believed did not grow nearer than 80 leagues. The hard and indigestible seeds swallowed by the Guacharo are found on the floor and ledges of the cavern in great quantities, and many germinate and grow for a short time in an etiolated condition, as I have mentioned the coffee seeds used to do in Malaya in caves haunted by civets. The Guacharo seems to be the only known bird which, like the fruit-bats, feeds on fruit at night.

PSITTACIFORMES.—PARROTS.

The parrots, lories, and cockatoos are largely fruit-eaters, but, in India at least, feed also very extensively on grain.

Palaeornis longicauda, the Malay long-tailed Paroquet, used to visit Singapore from the forests at irregular intervals in small flocks, plundering any trees in fruit. They ate figs (*Ficus benjamina*), and among other fruits the small green capsules of *Macaranga populifolia* (*Euphorbiaceae*). *P. torquatus*, the rose-ringed Paroquet of India, is very destructive to grain, but it feeds also on the arils of *Cephalandra* (*Cucurbitaceae*), the drupes of *Zizyphus jujuba*, and *Nephelium Litchi*, and figs (*Ficus* sp.).

P. schisticeps feeds on pomegranates and apricots; and *P. cyanocephalus* on figs of various species (Mason).

Psittinus cyanurus, of the Malay Peninsula and islands, according to Heyst, feeds on the fruits of *Macaranga rhizinoides* in north-east Sumatra.

Loriculus vernalis, the Indian Lovebird, feeds on guavas (Mason).

Nestor meridionalis, the Kaka Parrot of New Zealand, according to Sir W. Buller, lives on the flowering spadices of *Freycinetia Banksii*, and Guppy says we can legitimately suppose it eats the fruits also. *N. occidentalis* feeds on berries of *Coprosma pumila* and *C. nivalis*, and Buller states that the New Zealand parrots also eat the fruit of *Elaeocarpus dentatus*.

Platycercus auriceps, in New Zealand, feeds on the fruits of *Coriaria ruscifolia*, *Coprosma lucida*, and *Fuchsia excorticata*.

Stringops habrophilus, the Owl-Parrot, eats the fruits of *Coprosma sarmentosa* and the *Fuchsia* (Buller).

Ara Macao, the blue and red Macaw, according to Waterton, fed on the fruits of the Coucourite Palm of the Amazons.

Chrysotis caymanensis.—This Parrot is peculiar to the Grand Cayman Islands, West Indies. M. T. Nicoll (in "Three Voyages of a Naturalist") writes of it:—"This man (a farmer) told me that every morning, shortly after "daybreak, these parrots came down to his land to feed on the guavas."

Amazona oratrix, the Yellow-headed Parrot of the Tres Marias Islands, Mexico, is stated by F. Nelson (*U.S.A. Agric. Bull., Biol.*, 14, 1899) to feed on the fleshy pods of *Pithecolobium dulce*, the Madras thorn, a native of India, often used as a hedge plant in the tropics; and *Psittacula insularis*, of the same locality, he says feeds on sweet wild figs.

Conurus flaviventer.—In Jamaica this parrot eats the fruits of Fiddle-wood (*Citharexylon*), Burn-wood (*Rhus metopium*), figs, Pride of China (probably *Melia azederach*), *Pimento* and Prickly yellow (*Zanthoxylum*).

Of African parrots, Schonland (*Ann. Bot.*, xxxviii, 460) writes as follows:—"The only native Palm which reaches Cape Colony, *Phoenix reclinata*, is

" distributed in a narrow coast strip as far as the Bushman's River. The " reason for its limited extent is probably to be sought for in the distribution " in the fruiting season of birds, specially *parrots*, which disperse its seeds. " Bews has shown that, in Natal, tropical plants ascend from a narrow coast- " strip in the river valleys to more temperate climates with the aid of birds." He does not give the name of the parrots.

FALCONIDAE and STRIGIDAE.

These birds are all carnivorous, and play little or no part in dispersal of seed. Seeds of weeds, however, have been found by Dr. W. E. Collinge in castings of the Little Owl (*Athene noctua*), probably swallowed in the stomachs of mice or birds, and T. E. Gunn records the occurrence of 2 yellow berries in the stomach of a Kite (*Milvus*). These birds also indirectly disperse grain and small seeds by tearing to pieces pigeons and other birds, and strewing the contents of their crops about (*see under* Pigeons, p. 497).

Wallace (in the " Palms of the Amazons ") says that the Vultures (Turkey-buzzards) *Cathartes*, occasionally eat the pulpy fruits of the Palm (*Astrocaryum murumuru*) when hard-up for other food.

Heinitz (in " Roffägler som fridspore," *Botan. Notiser*, 1916, 127) gives an account of seeds found in the stomachs of some birds of prey, instancing *Alchemilla vulgaris* and *Betula odorata* (*B. pubescens*) in the Goshawk (*Astur palumbarius*); *Galeopsis* nucules in the Sparrow-hawk (*Accipiter nisus*); and 8 seeds of *Paris quadrifolia* in a Hawk-owl (*Surnia Ulula*). These were probably all swallowed in the prey of the birds.

FREGATIDAE.—Frigate Birds.

Fregata aquila, Greater Frigate-bird.—Mr. Clunies Ross, of Cocos-Keeling Island, informed me that these birds, when the boobies are not nesting, and they are unable to procure their ordinary food, which consists of fish taken from the boobies, swallow seeds of *Guilandina bonduc* and beans, which they find floating in the sea, and on flying to the land vomit them up again, either using them to temporarily fill the stomach, or perhaps in place of gravel for digestive purposes. The round smooth seeds of the *Guilandina Bonduc* and *G. bonducella* are undoubtedly sea-dispersed, but I have found the plants a considerable distance inland, where they cannot have been drifted up by the sea, and Guppy found the same in Hawaii, not on the beach, but from between 100 yards to a mile from the sea.

ANATIDAE.—Ducks, Geese and Swans.

All these birds fly to immense distances and at a very rapid rate. Some species of ducks appear to visit almost every part of the world, and as they can easily rest on the water, if tired, are able to cross extensive tracts of sea. A duck has, on several occasions, visited Christmas Island, 194 miles from Java, though there is no fresh water for it to rest on, and it has had to swim in the sea. Flights of *Dendrocygna* regularly reach Cocos-Keeling Island, 700 miles from Java.

All the species feed largely on herbage, fruits, and seeds, and convey a large quantity of seeds about in their viscera, though perhaps, to a larger extent, on their bodies and feet. They feed on various fruits and seeds, especially of aquatic or marsh plants on or near a pool or river, and then fly to another, only descending in a similar locality unless injured or sick. Here they deposit the seeds they have brought from the previous pool,

and, after feeding again, move on to a further one. By this means a plant may move on from pool to pool, or river to river. Some waterfowl remain a long period at or about one spot, but many migrate, according to season, or, on the Equator, quite irregularly. In the Singapore Gardens the big lake was often visited by Tree-teal (*Dendrocygna*), Goose-teal (*Nettopus*), cormorants, jacana, small blue herons, and sandpipers. Usually these birds only stayed a day or two, or perhaps a week, and flew on to the next piece of water—the reservoir, some miles away—and then moved on from there to some other place. In this way these birds can carry seed internally—or attached to feathers or feet—rapidly across a continent from north to south, and from the south northwards.

I have little doubt that the very wide distribution of aquatics and many small-seeded marsh-plants is due to the migrations of these birds. This part of the work deals only with seeds swallowed by ducks and passed from the intestines. These birds, like most others, are liable to attacks from falcons, eagles, etc., and also from shooters, and may be killed with a full crop of food, the seeds germinating in the remains of the bird, or being scattered when it is torn to bits. In this way seeds, e.g., acorns, which would be destroyed by digestion, might be left at some distance from the original tree in a germinable state.

The ducks, swans, and geese swallow large quantities of seeds of aquatic- and marsh-plants, but it has been suggested that most, or all of these, are destroyed in the process of germination. Guppy, however, writes (" Naturalist in the Pacific," ii, 369, 370) :—" About 12 years ago I examined the stomachs " and intestines of 13 wild ducks obtained in the London market. Three " of them contained in all 41 seeds of *Potamogeton*, most of which subsequently " germinated in water. In one of my experiments, in December, I fed a " domestic duck with the fruits of *Potamogeton natans*. They appeared in " quantity in the droppings, for the most part divested of their soft coverings, " but otherwise uninjured. Sixty per cent. germinated in the following spring, " whilst of those left in the vessel from which the duck had been fed, only " 1 per cent. germinated in the next spring, and another year elapsed before " any number did so. My experiment showed that 7 to 8 hours at least " were occupied by *Potamogeton* nutlets in passing through the digestive canal " of the duck, and probably 9 to 10 hours with an average full meal. But this " does not represent the possible maximum period, since the hard stone may " remain in the gizzard for a long time with the ordinary gravel."

Considering the rapid flight of a duck when migrating, this period would be sufficient for it to transport the seeds to most oceanic islands.

On p. 513 of the same work Guppy writes :—" Out of 13 wild ducks " obtained in the London market, and stated to have been sent from Norfolk " and Holland, 11 contained in their stomachs and intestines 828 seeds :—

295 seeds of *Sparganium* in	..	..	8 birds.
41 ,, *Potamogeton* in	..	..	3 ,,
270 ,, *Cyperaceae* in	..	..	5 ,,
222 not identified.			

In the case of 4 birds the germinating capacity of the seeds was tested and in three cases very successfully ; the seeds of *Potamogeton*, *Sparganium* and the *Cyperaceae* germinated readily in water.

Dr. Schenk (" Der Biologie der Wassergewachse," 1886) states that he fed tame ducks with water-lily seeds, and found that in a short time they thoroughly digested the seeds. *Nuphar lutea*, and other species of the genus, have an ovoid green fruit about 2 inches in diameter, which, when ripe, separates from the peduncle, and the pericarp splits into 9 or 10 strips exposing

the seeds contained in crescentic white masses, resembling the pips of an orange, and each containing about 16 yellowish-brown seeds. The pips float, and are very conspicuous when in the water. I gave some to some ducks, tufted duck and pochard, who seized them and appeared to suck the contents and abandoned the skin. A large carp came to the surface and took one down, also returning the skin. The pips when left alone float for some days, then seem to dissolve and the seeds sink. Most of the dissemination of these plants is effected undoubtedly by the floating of the pips, but I do not understand how such species as *Nuphar pumila*, etc., appear in isolated lakes, unless conveyed internally safely by ducks.

It may be stated that practically all ducks to some extent feed on berries, drupes, seeds and bulbs of aquatic and often terrestrial plants, some are exclusively vegetarian, but most eat also water-snails, insects, and sometimes small fish, frogs, etc. It is largely to these birds that the wide distribution of many aquatic plants is due. They fly fast and far, often crossing the sea for considerable distances up to 700 miles.

Anas boschas, Wild Duck.—As mentioned already, Guppy examined the contents of the viscera of 13 specimens obtained in the London market and found large numbers of seeds of *Sparganium*, *Potamogeton* and *Cyperaceae*, which germinated readily.

Thompson (in " Morris's British Game-Birds," ed. ii, p. 223) records a case of 4,500 seeds of *Zostera marina* being found in the stomach of a mallard. The testa of these seeds is membranous, and it seems probable that they would be digested by the duck, but some might pass unharmed. Birger says that in the crops of the wild duck in Sweden he found seeds of *Carex Goodenovii*, *Empetrum nigrum*, *Vaccinium myrtillus*, *V. uliginosum*, *V. vitis-idaea*, *Ranunculus repens* and *R. acris*, *Rumex*, probably *R. domesticus*, *Menyanthes trifoliata* and *Juncus bufonius*, and over 100 bulbils of *Polygonum viviparum*; and Newstead records finding the crop of a mallard filled with 300 or 400 seeds of *Galium aparine*.

This bird, which is one of long-range flight, appears mainly vegetivorous, and probably plays a large part in the dispersal of aquatic or riparian plants.

Anas platyrrhyncha, the American Mallard.—McAtee (in *U.S.A. Bull. Agric.* 720) gives an account of the food of the American Mallard, and also refers to this bird in " Eleven Important Duck Foods " (*Bull.* 205, 1915). In the latter paper he mentions that *Characeae* are eaten by 14 species of duck. These doubtless swallow the seeds and so disperse them. He gives the following plants as eaten specially by the American mallard (in these and other cases the food was found in the stomach of a bird, and I select merely those which could readily pass through it with the seed unharmed): *Sparganium androcladum* and *S. eurycarpum*, *Potamogeton lucens* and *P. praelongus*, *P. foliosus*, *P. Friesii*, *P. pusillus*, *P. pectinatus*, *Ruppia maritima*, *Zannichellia*, *Zostera*, *Naias flexilis*, *Triglochin maritimum*, *Echinodorus*, *Alisma plantago* and *Sagittaria* (4 species) (perhaps these *Alismaceae*, having mostly dry achenes, would be destroyed in transit), many grasses and sedges, *Cyperus ferax*, *Scirpus cubensis*, *Fimbristylis*, *Cladium effusum* and *C. mariscoides*, *Rhynchospora* and *Carex* (5 species) being the most abundant; *Pontederia cordata*, *Thalia*, *Myrica cerifera* and *M. caroliniensis*, *Planera aquatica*, the Water Elm (*Urticaceae*) (a bird was found with 200 seeds of this in its crop; the fruits of this tree fall in the water before they are ripe, and dehisce in the water; it has a burr-like husk with processes), *Polygonum* (10 species), *Chenopodium album*, *Salsola*, *Atriplex*, *Salicornia*, *Phytolacca decandra*, *Rivina humilis* (a herb with scarlet berries), *Portulaca oleracea* (the wide distribution of this plant, which has dehiscent capsules with small seeds, is rather remarkable; there is no doubt that it owes much of its world-wide distribution to human agency, but, so far as I can see, that will not

account for all), *Ranunculus*, *aquatilis* section (4 species); *Ceratophyllum*, 150 seeds in one crop (a plant of almost world-wide distribution; all ducks appear to be fond of it); *Brasenia Schreberi* (abundant), *Cabomba* (rare), *Nuphar advena*, *N. polysepala*, *N. americana*, *Nymphaea mexicana* (eaten by most ducks); *Liquidambar*, *Platanus*, *Rosa*, *Rubus*, *Crataegus* (many), *Croton* and *Euphorbia*, *Rhus glabra*, *R. radicans* and *R. toxicodendron*, *Ilex vomitoria*, *I. decidua* and *I. verticillata*, *Cardiospermum halicacabum* (*Sapindaceae*) (the Balloon Vine is now widely distributed over the world, but it owes something of this to human agency, as it is used as a vegetable and for basket-making; the loose pods also float on water); *Vitis* sp., *Passiflora incarnata*, *Opuntia*, *Decodon verticillatus* (*Lythraceae*) *Hippuris*, *Proserpinaca pectinata*, *Myriophyllum verticillatum*, *Hydrocotyle*, *Cicuta*, *Cornus* (6 species) (most ducks eat these); *Gaylussacia baccata*, *Diospyros virginiana* (not common; it is a tree, and the ducks could pick up only the fallen fruit); *Styrax americana* and *S. pulverulenta*, *Adelia acuminata*, *Menyanthes trifoliata* not very common (the Bog-Bean is, I believe, largely dispersed by ducks in England, as it constantly occurs in ponds and places where wild ducks breed. It has a greenish pulpy fruit); *Forestiera acuminata* (*Oleaceae*) Swamp Privet (it has a blue watery berry $\frac{1}{2}$ to $\frac{3}{4}$ inch long. *Aix sponsa*, the Wood Duck, eats more of this than the mallard, probably because it gets at the crop in the woods quicker than the mallard); *Heliotropium indicum*, much eaten by mallards, but it may be doubted if the nutlets pass through intact; *Verbena*, *Plantago* (not common); *Cephalanthus occidentalis* (much eaten by all ducks); *Diodia virginiana* and *D. teres*, *Triosteum perfoliatum* and *Symphoricarpus racemosus*. *Limnobium spongia*.—Of this water-plant McAtee states (in the paper on " Eleven Important Duck Foods "):—" The berry contains " a mixture of seeds and a gelatinous substance. 18 per cent. of the food in the " stomachs of 308 mallards consisted of this, and from 8,000 to 10,000 and " in one case 32,000 seeds were contained in the crop." It is a floating aquatic (*Hydrocharidaceae*), the seeds when dry possess short spines which possibly serve to attach it to mud, and it may be also carried about on the feet of birds. There are 3 or 4 species of the plant, all American.

Anas rubripes, the American Black Duck.—The food of this is catalogued also by McAtee in the paper on the food of the mallard. It appears to feed on most of the fruits mentioned above, and in addition on:—*Eriocaulon* sp., *Sesuvium maritimum*, *Empetrum* (occasionally), *Vaccinium*, *Lippia nodiflora*, *Potamogeton perfoliatus*, *P. foliosus* and *P. pectinatus*; but no other species are recorded, no *Cyperaceae*, except *Cladium*, and a good many other plants found in the mallards' stomachs are not recorded, probably because fewer birds were examined.

A. fuligula, the Southern Black Duck, seems to be scarcer, and fewer plants are recorded as food for it. They are *Ruppia*, *Naias flexilis*, *Rhynchospora*, *Scleria*, *Peltandra virginica* (*Aroideae*), *Pontederia cordata*, *Myrica*, *Ceratophyllum*, *Nuphar* and *Nymphaea*, *Vitis* sp., *Hippuris*, *Heliotropium indicum*, *Cephalanthus occidentalis* (Marrott).

Mr. Douglas C. Marrott (*U.S.A. Dept. Agri.*, *Bull.* 862, 1920) gives an account of the food habits of 7 species of shoal-water ducks, viz., the gadwall, bald-pate, widgeon, green-winged teal, blue-winged teal, pintail and wood duck, from which paper I extract such material as has bearing on our subject.

Chaulelasmus streperus, the Gadwall.—This bird breeds in Northern Europe, Asia, and North America, ranging south in winter to Southern Asia, some way into Africa, and as far south in America as the southern end of California, and as far east as China and Japan. In fact it ranges over the whole of the temperate zone. It feeds largely on aquatic vegetation. About half the food taken by this bird was found to be Naiadaceous plants, especially *Potamogetons*. The plants eaten were:—*Potamogeton* sp., *Ruppia maritima*,

Zannichellia palustris, *Naias flexilis*, *Zostera marina*, *Scirpus americanus*, *S. paludosus*, *S. maritinius*, *Cladium effusum*, *Cyperi* sp., *Ceratophyllum demersum*, *Chara* sp., *Polygonum lapathifolium*, *P. amphibium*, *P. aviculare*, *P. pennsylvanicum*, *P. hydropiper* (in one stomach 3,000 seeds), *P. persicaria*, *P. hydropiperoides*, *P. sagittatum*, *P. convolvulus*, *P. pelousanum*, *Rumex* sp., *Vallisneria spiralis*, *Philotria* sp., *Castalia* sp. (*Nymphea*), white Water-lily (in one stomach 1,200 seeds), *Brasenia Schreberi* (a water-lily with hard seeds), *Cephalanthus occidentalis*, *Salicornia ambigua*, *Vitis* sp., *Celtis* sp., *Ilex* sp., *Rhus radicans* (Henderson), and other species, *Bidens*, *Myriophyllum*, *Hippuris vulgaris*, *Ranunculus* sp., *Hydrocotyle*, *Cuscuta*, *Myrica*, *Sparganium*, *Heliotropium indicum*, and various grasses.

I exclude from the list plants like *Lemna*, and tubers of *Sagittaria* which, though eaten, could hardly pass through the alimentary canal alive. A great many of these plants, especially the *Naiadaceae* and grasses, are eaten for the foliage, but seeds are swallowed and probably in many cases pass through the intestine safely.

Marica americana, the Bald-pate.—This is entirely an American duck, breeding in the northern parts of America. It ranges in the winter to Florida, Cuba, Jamaica, Porto Rica, Trinidad, Guatemala, and Costa Rica. It eats the same plants as the gadwall, but consumes less seed. In addition to most of the plants eaten by the latter bird, Marrott records the occurrence in the stomachs of the Bald-pate—*Scirpus fluviatilis*, *Heleocharis* sp. (in one stomach 64,000 seeds), *Cladium mariscoides*, *Carex* sp., *Fimbristylis* sp., *Triglochin maritimum*, *Nymphaea* sp., *Atriplex* sp., Saltbush, *Portulaca* sp., *Rubus* sp., *Melilotus* sp., *Medicago denticulata*, *Croton* sp., *Cicuta* sp.

Mareca penelope, Widgeon.—This bird extends all over Europe and temperate Asia, and in the winter goes as far south as Egypt. It is less frequent in America, but is recorded from Virginia, North Carolina, Massachusetts, and both Atlantic and Pacific coasts. The records of the few specimens examined by Marrott, give :—*Ruppia maritima* (known as Widgeon Grass), *Cuscuta* sp., *Sparganium* and *Scirpus robustus* for North America. Birger found many achenes of *Ranunculus acris* in the crop of one killed in Norway.

Nettion carolinense, Green-winged Teal.—This is strictly American, and occurs all over North America, migrating to Mexico, Bahamas, Cuba, Jamaica, Honduras, Tobago. It feeds largely on seeds, especially on those of *Cyperaceae*, and, in addition to those already recorded, eats the seeds of *Rhynchospora* and *Scirpus cubensis*. As many as 30,000 seeds of Cyperus were found in one stomach, and *Heleocharis* and *Fimbristylis* reached as high as 1,000 in a stomach. Of the *Potamogetons*, the most common was *P. pectinatus*. Grass seeds were commonly eaten, chiefly of the genus *Panicum*, *Echinochloa crus-galli*, and *E. colona*, of which 6,000 seeds were found in one stomach. *Zizania palustris*, *Zizaniopsis miliacea*, *Setaria glauca*, and other species, and *Monanthochloa littoralis*. *Polygonums* were very abundant. Of the species already recorded, one bird had eaten 1,630 seeds of *P. aviculare*. *Charas* were especially favoured, and the fruits persisted, often in thousands, in the stomach after all other parts of the plant had been digested. Of *Proserpinaca*, Mermaid Weed, seeds were found in one gizzard (Marrott). It eats also the fruit of *Rhus radicans* (Henderson).

Querquedula discors, Blue-winged Teal.—This is also confined to America, but besides occurring all over North America, migrates in winter to Brazil, Ecuador, Peru, and Chile, as well as Mexico and the West Indies. It feeds on the same plants as the previously-mentioned ducks, with the recorded additions of :—*Dulichium* sp. (*Cyperaceae*), *Homalocenchrus oryzoides*, *Puccinellia Nuttalliana*, *Sporobolus* sp., *Spartina* sp., *Polygonum portoricense*, *Galium* sp., *Diodia teres* (*Rubiaceae*). Twenty-eight other families of plants were represented, including *Compositae*, *Alismaceae*, *Umbelliferae*, *Boragineae*, *Rosaceae* and *Verbenaceae* (Marrott).

Querquedula crecca, Teal.—The teal feeds on the fruits of *Carex*, *Heleocharis*, *Juncus*, and *Comarum palustre*, according to Holmboe, in Scandinavia, and Briger adds :—*Carex Goodenovii* and *Empetrum nigrum*. Theobald says in India they feed on all kinds of grasses and their grains.

Q. cyanoptera, Cinnamon Teal, occurs in both North and South America. It feeds on much the same plants as most of the American ducks do, and in addition Marrot records seeds of one of the *Malvaceae*, *Chenopodium*, *Amaranthus*, *Ranunculus delphinifolius*, and *Trifolium* sp.

Dafila acuta, Pintail.—This duck occurs all over the whole north temperate zone, migrating south to North Africa, to Persia, China, and Japan, and North America to Cuba and Panama. It feeds largely on fruits of *Naiadaceae*, including *Potamogeton pectinatus*, *P. pusillus*, *P. foliosus*, *P. diversifolius* and *Cyperaceae*. Marrott records finding 15,000 fruits of *Rhynchospora*—3,000 of *Scirpus*, 3,600 *Heleocharis* and 900 *Scirpus cubensis*—in stomachs of this bird respectively, and also fruits of *Rhynchospora corniculata*, *Limnobium spongia*, *Polygonum punctatum* (12,500 seeds in one gizzard). *Salicornia ambigua* and *Sambucus* seeds have also been found in its stomach. In India it eats wild rice and various aquatic plants.

Fuligula clangula, Golden Eye, feeds on fruits of *Potamogeton natans* (Holmboe). This is also a wandering bird. It is said by Stuart Baker to eat deep-water weeds in India.

Aix sponsa, Wood Duck.—This duck occurs in North America, Cuba, Bermuda, Mexico and Jamaica. It not only frequents the open waters and marshland, but the banks of wooded streams and ponds, where it feeds on seeds of plants growing near the water, and also wanders far out into drier parts of the woods to pick up acorns, nuts, grapes and berries. The following are seeds, not recorded as food for other ducks, found in the stomachs of wood-ducks :—*Carex decomposita* and *C. lupuliformis*, *Glyceria nervata* (5,300 to 10,000 seeds in one gizzard), *Eragrostis* sp., *Potamogeton zosterifolius*, *Quercus* (several species), *Nuphar advena* and *N. microphylla*, *Nymphaea odorata* and *N. tuberosa*, *Planera aquatica* (*Urticaceae*), *Ulmus* sp., *Boehmeria cylindrica*, *Peltandra virginica* and *Symplocarpus foetidus* (*Aroideae*), *Ambrosia trifida*, *Sparganium eurycarpum*, *Limnobia*, *Fraxinus americana*, *Adelia acuminata*, *Sagittaria latifolia*, *Saururus* (stomach contained up to 10,000 seeds), *Jussiaea* sp., *Pontederia cordata*, *Lippia* sp., *Decodon verticillatus*, *Berchemia scandens*, *Rhamnus catharticus*, *Nyssa sylvatica*, *N. aquatica*, *Cornus* sp., *Styrax* sp., *Crataegus* sp., *Liquidambar styraciflua*, *Smilax*, *Forestiera acuminata*, Swamp Privet (*Oleaceae*) (Marrott).

Spatula clypeata, the Shoveller.—Henderson says this feeds on the fruits of the Poison Ivy (*Rhus radicans*) in North America.

Taking the ducks as a whole class, it will be readily seen of what vast importance these birds are to dispersal of marsh and aquatic plants, and notably of the *Cyperaceae*, the other means of diffusion of which seem so poor. Ducks fly over the whole world area, from the Arctic regions to the Antarctic, and travel at a very rapid rate. They are very voracious, and swallow large quantities of seed. Many dive to the bottom of the water and pick up non-floating seeds. They are often attacked and torn to pieces by large falcons, eagles and foxes, so that the seeds they have swallowed may be scattered far from where they picked them up. Many seeds and small aquatics, as well as portions of larger ones, adhere to their bodies and feet, and are so transported. It is to these wandering birds that we undoubtedly owe most of the extremely wide distribution of the marsh and pool sedges and grasses and aquatic plants.

Anser.—The Domestic Goose is said by Huth to disperse the seeds of *Potentilla anserina* (*Rosaceae*), the birds being fond of the foliage, and, in eating it, swallow and pass the seeds.

Wild geese, according to Ekstam, are hearty plant-eaters in Spitzbergen, and he found in their droppings fruits of *Oxyria reniformis* and an abundance of bulbils of *Polygonum viviparum*, some of which proved to be capable of growth (Tromso Museums Aarshefter xviii–xx, 1895–1897). *Anser hyperboreus*, according to Holmboe, eats the fruits of *Potamogeton natans* and *Empetrum nigrum;* and *A. cinereus* the fruits of *Rubus Chamaemorus* in Sweden. They feed largely on grain, leguminous seeds generally, and eat acorns, but they probably destroy almost all of these seeds in digestion, or by biting them up. I found, however, in Kew Gardens, excreta of geese full of quite uninjured grains, including maize.

Chloephaga magellanica, Upland Goose of the Falkland Isles, feeds on berries of *Empetrum rubrum* (Valeton, "Notes on Falkland Isles," Manchester Memoirs, 1904, 37).

Bernicla sandwicensis, the Hawaii Goose, according to Guppy, feeds largely on fruit. "The berries of *Vaccinium reticulatum* are known to be the principal food of the mountain goose." He also records finding in the stomach of one of these geese a number of the stones of *Cyathodes tamaiameiae* (*Santalaceae*), and says that Hillebrand and other authors affirm that *Fragaria chilensis* is much appreciated by this bird. Hillebrand states that it also eats the drupes of *Coprosma ernodiodes*, and Guppy has found the stones of this fruit in its stomach ("Naturalist in the Pacific," p. 282).

Branta bernicla, the Brent Goose, feeds largely on *Zostera marina*, and it has been suggested that it may be responsible for the dispersal of this sea-wrack.

Cygnus olor and *C. minor*, the swans, are both recorded as feeding on the fruits of *Potamogeton natans* (*see* p. 337), and Mason says that in India all the swans feed on seeds of aquatics.

ARDEIDAE.

The Herons and Storks feed on fish, frogs, and other animal food, but in swallowing fish they may also swallow and convey to a distance seeds eaten previously by the fish. Darwin quotes Audubon as saying that he found seeds of the great Southern Waterlily (probably *Nelumbium luteum*, according to Hooker) in the stomach of a heron. As Darwin suggests, it would (perhaps after flying a considerable distance) have disgorged the seeds in a pellet, fit for germination.

GRUIDAE.

The common Crane (*Grus grus*) is stated by Holmboe to feed on fruits of *Vaccinium vitis-idea* in Scandinavia, and on Water-melons (*Citrullus vulgaris*) in India (Mason).

OTIDIDAE.—Bustards.

Eupodotis Edwardsi, the Indian Bustard, eats the fruits of *Zizyphus jujuba* and *Carissa carandas* (Mason).

Houbara Macqueenii, also an Indian bird, feeds on fruits of *Zizyphus jujuba* and *Grewia* (Mason).

Chariotes Kori, Great Bustard of the Transvaal.—" When the berries of " the Resyntjebos (Rosyntjiebos is given as meaning *Grewia cana* and *G. flava*) " are ripe, these birds feed almost entirely on them " (A. Roberts, " Birds and Mammals from the Transvaal," *Ann. Transvaal Mus.*, xii, 289).

Afrotes afraioides feeds on the seeds of the creeping everlasting *Helichrysum argyrosphaerium* in the Transvaal (A. Roberts).

OPISTHOCOMIDAE.

Opisthocoma cristatus, the Hoazin.—This remarkable bird lives in the swamps and creeks of Guiana, Venezuela, and the Amazons. According to Bates (" Naturalist on the Amazons," Chap. iv) it feeds on the fruits of the sour guava (*Psidium acre*), and other wild fruits. " The natives say it devours " the fruits of arborescent Arums, *Caladium arborescens* (*Montrichardia arborescens*, " and *M. aculeata*), which grow in crowded masses round the swampy banks " of the lagoons." W. Beebe confirms this, and gives an account of the birds nesting among these plants. The *Montrichardia* is called " Muka-Muka " by the natives. It grows from 10 to 25 feet in height, in the water-streams, lagoons, and rivers (chiefly tidal), and inland in pools and creeks. The fruit is an oblong head of berries as big as a fair-sized potato, first green, then becoming yellow. The seeds are globose, as big as marbles (Jenman).

CHARADRIDAE.—Waders.

Most of these birds eat only animal food. They play a part, however, in seed dispersal by conveying seed in mud on their feet, as described under that section, but a few also devour seeds and fruits.

Squatarola cinerea, Grey Plover, and *Charadrius pluvialis*, the Golden Plover, are said (Meyer, " British Birds ") to feed on the fruits of *Vaccinium* and *Empetrum*.

Numenius arquatus, the Curlew, according to Holmboe and Meyer, eats Bilberries (*Vaccinium myrtillus*). H. St. John, in an account of Sable Island in North America (Contrib. Asa Gray Herb. 1921, xxxviii), says of *Empetrum nigrum* :—" The berries form a part of the food of the birds that visit the island, " especially the curlews."

N. tahitensis inhabits Alaska, migrating south to Hawaii, Tahiti and Paumotu. Peal notes that in the latter island the fruits of a species of *Canthium* (probably *C. odoratum*) forms the principal food of the bird (Wilson, *Aves Hawaienses*).

In a number of these waders, *Sarcogrammus indicus*, Indian Lap-wing, *Limosa belgica*, *Totanus glareola*, *Gallinago nemoricola*, and *G. coelestis*, etc., small seeds have been found in the crops, apparently accidentally picked up, according to Mason.

LARIDAE.—Gulls and Terns.

These birds eat fruit to some extent, and may possibly be responsible for some plants occurring in oceanic islands, but most of the islands which are visited by sea-birds only, do not contain plants with drupes or berries. Ekstam states that species of *Larus* consume greedily all kinds of berries in the North European region, and especially those of *Empetrum nigrum*, the seeds of which have been found in their droppings, by Prof. Lagerheim, in Arctic Norway. Holmboe records *Larus marinus*, the Black-backed Gull, as eating the fruits of *Rubus Chamaemorus* in Sweden. M. M. Portel (in the *Field*, September, 1927) writing of the destructiveness of gulls (presumably the Black-headed Gull, *L. ridibundus*), says they devour large quantities of oat and corn grains, and their castings contain many undigested grains of oats. As these birds have taken largely to a land life, and have become granivorous, they may disperse other weed seeds.

H. O. Forbes (in " A Naturalist's Wanderings ") says of the little White Tern (*Gyges candida*) in Cocos-Keeling Island :—" The old birds often feed " on the Papaya fruit, hovering on their wings all the while like honey-suckers

"at a flower." This bird ranges the sea to islands as far apart as Fernando de Noronha and Cocos-Keeling Island.

STERCORARIDAE.—The Skuas.

Stercorarius parasiticus, Buffon's Skua, is recorded by Holmboe as feeding on fruit of *Vaccinium vitis-idea* and *Empetrum*, in Sweden; and *S. crepidatum* to eat bilberries, *Vaccinium myrtillus*, *Arctostaphylos alpinus*, and *Rubus Chamaemorus* and *Empetrum nigrum*.

PROCELLARIIDAE.—Petrels.

Daption capense, the Cape Pigeon.—Hemsley (in the Introduction to the Botany of the Challenger Expedition, p. 45) records the finding of a small hard seed in the gizzard of this bird 550 miles from the east of Tristan d'Acunha. The birds, however, follow ships to pick up scraps thrown overboard, and it may have picked up the seed from waste from a ship.

Procellaria glacialis, Fulmar Petrel.—"Sir W. Milner cut open some young "nestling fulmars at St. Kilda, and found large curious nuts in their crops, "I suspect picked up by parent birds from the Gulf Stream" ("Darwin's Life and Letters," ii, 147). Mr. C. Dixon ("Ibis," 1885) says that he found a seed in the crop of one of these birds from the same locality. Unfortunately these seeds were never identified.

PODICIPEDES.—Grebes.

Podicipes cristatus, the Great Crested Grebe, feeds on the fruits of *Nuphar luteum*, and *Nymphaea alba* in Scandinavia (Holmboe). This bird is a great wanderer, and may be responsible to some extent for the dispersal of the water-lilies.

Wetmore (in "Food and Economic Relations of North American Grebes") records finding a seed of *Nymphaea* in the stomach of *Colymbus dominicus*, and one of a *Polygonum* in *C. nigricollis*, and seed of Ragweed (*Ambrosia*) and of *Bidens* in that of *C. auritus*. All these seeds seem to be swallowed accidentally while the birds are fishing for the mollusca, water insects, and fish which they live on.

RALLIDAE.—Rails.

Porphyrio melanotus, New Zealand Swamp Hen.—In Sir W. Buller's "History of the Birds of New Zealand" we read that, when the *Coprosma* (*Rubiaceae*) is in fruit, the swamp hens come out to eat it. *P. vitiensis*, of New Caledonia, according to Layard, feeds on maize, etc. ("Ibis," 1822). Guppy records (l.c., p. 296) that in a specimen of a *Porphyrio* shot in Fiji he found the stomach full of the stony fruits of *Scleria* (*Cyperaceae*). The bird had probably been eating the whole plant and swallowed the seeds with it; but in one species of the genus the disc which supports the small, stony black fruits is fleshy and red, obviously as an attraction to birds. Most of the species grow in Malaya in dry spots where these gallinules do not go, though some are swamp plants.

Rallus aquaticus, Water Rail, feeds on berries of *Vaccinium* in Scandinavia (Holmboe). Newstead found 9 seeds of *Rosa* in the crop of one in England. Macgillivray says it eats grass seeds. *R. philippensis.*—According to Buller, in New Zealand this rail climbs up the scandent *Freycinetia Banksii*, and eats the fruit.

Gallinula chloropus, Moorhen.—This certainly lives mainly on mollusca

and insects, and also grass blades. Newstead records finding the seeds of blackberry in the crops of young birds; this is very curious, as by the time the young birds were hatched there could not have been any blackberries left, except dead and dried ones from the previous autumn.

Ocydromus Greyi, the Weka Rail or Wood-hen of New Zealand, according to Buller, eats the fruits of *Fuchsia excorticata* and *Coprosma lucida*; and *O. Earli* feeds also on *Rubus australis*.

Fulica atra, the Coot, a far-flying bird, is said also to feed on fruits of aquatic plants.

In Mason's "Food of Birds in India," he mentions from various sources the following birds as being known to swallow small seeds:—*Hypotoenidia striata*, Banded Rail, *Porzana parva*, *P. pusilla*, *P. marnetta*, *Amaurornis fuscus* and *A. phoenicurus* (*Leguminous* seeds) and *Gallicrex cinerea*, the Watercock.

The importance of the rails lies in the extraordinary distances that these apparently weak-flighted birds go, and the fact that few oceanic islands are without them. Rails occur in Tristan d'Acunha, Christmas and Cocos-Keeling Islands.

COLUMBIDAE.—PIGEONS.

The pigeons and doves are the most important dispersers of seeds of any group of birds. They are voracious eaters of berries, drupes, and grain, and fly very long distances, not only over land, but far over the sea, and they move very fast, so that they can disperse seeds swallowed, at a very great distance from the spot from which they took them. They occur all over the world in hot and cold climates, and often move in large flocks. There is hardly an oceanic island that they do not visit. Fernando de Noronha contained one very abundant species, *Zenaida*, and Christmas Island 3—*Carpophaga*, *Myristicivora*, and *Chalcophaps*; the Azores have *Columba*.

In the north temperate regions, Europe and North America, where cereals are largely cultivated, these birds feed extensively on grain and the seeds of the cornfield weeds, most of which are destroyed by the digestive process, as are also the acorns and beech-mast and nuts which they swallow; but the pigeons form a large part of the food of the bigger hawks, who tear numbers of them to pieces when returning to roost with a crop full of grain and seeds, and strew these seeds about in an excellent condition for germination. Besides these dry fruits and seeds they also, especially in hard frosts, consume considerable numbers of berries.

In the tropics, where cereals other than rice are not, or hardly ever, cultivated, the pigeons and doves live mainly on berries and drupes, and, unless the seeds be too large, they swallow and pass them; otherwise they disgorge them, as do blackbirds and thrushes, after removing the pulp or, in case of arillate seeds, the arils. They may be classed as forming the most important seed-dispersers in the world.

Columba palumbus, the Wood-pigeon.—The feeding of this bird has been well studied in England. It is very common, and flies very rapidly to long distances.

Its food consists largely of acorns and beech-mast. As long as it can get these it appears to eat nothing else. C. St. John ("Wild Sports in the Highlands") writes:—"When acorns are plentiful, the wood-pigeons seem to "prefer them to anything else, and the quantity they stow away in their "crops is perfectly astonishing." In Kew Gardens a number of these birds arrive in October and November for the acorns and beech-mast, and remain till all are eaten. They feed here on *Quercus Robur*, *Q. cerris*, and a little later on *Q. ilex*, the Holm Oak, and also on beech-mast. A. S. Watt ("Failure of Regeneration of Beech," in *Oecol. Journ.*, 1923, 12) says:—"The most serious

"enemy of the beech is the wood-pigeon. Sussex woodmen record cases "of pigeons being found dead with their crops distended with beech-mast, "and throats inflamed, possibly irritated by the sharp edges of the three- "cornered nut." When the acorn crop is not available they feed largely on grain and seeds picked up in the fields, and at some times, especially severe winters, feed on berries and drupes.

In winter and early spring they eat the fruits of holly and ivy. St. John says :—"They feed on fruits of all kinds (in Scotland), both on the wild berries, "Mountain Ash (*Pyrus aucuparia*), ivy, etc., and almost all garden fruits that "are not too big to be swallowed. Numbers come every evening to my "cherry trees, where they fearlessly swallowed as many cherries as they could "hold." Collinge quotes from several authors who state that they have found in their crops, besides the above-mentioned fruits, bilberries and gooseberries. They feed also very extensively on weed-seeds, and S. P. Mercer (*Journ. Board. Agric.*, 1918, p. 977) records his finding 8,000 seeds of *Atriplex patula* in the crop of one bird. Woodruffe-Peacock (*Selborne Mag.*, xxix, 29) describes the results of an attack on the wood-pigeons by peregrine falcons. He states that in his district (Lincolnshire) 40 pigeons were killed by the falcons between December 7th and January 7th, and many of the birds had the crops full of seed. The contents of a crop may weigh as much as 4 ounces. He records the contents of the crops of two birds.

No. 1.—Bird killed in the evening with a very full crop, containing the following seeds, which were germinating or on the point of doing so when found:—*Chenopodium album*, *Brassica arvensis*, *Cytisus*, *Plantago major*, *P. lanceolata*, *Polygonum aviculare*, *Viola arvensis*, *Linaria vulgaris*, *Lycopus europaeus*, *Convolvulus arvensis*, *Melilotus arvensis*, *Ulex europaeus*, *Spergularia arvensis* and the var. *sativa*, *Anagallis arvensis*, *Cerastium vulgatum*, *C. arvense*, *Lysimachia vulgaris*, *Lychnis alba*, *Carduus nutans*, *Cichorium intybus*, *Geranium molle*, *Urtica urens*, *Thlaspi arvensis*, barley and wheat.

No. 2.—Acorn, beech-mast, hawthorn, *Papaver rheas*, *P. dubium*, *Brassica alba*.

I have myself seen a dead wood-pigeon in Herefordshire (killed by a hawk), the crop of which was full of germinating oats and wheat, and similar cases are recorded where the crop was full of germinating beans. Before hawks and falcons were regularly persecuted by gamekeepers and others, they must have been very much more abundant, and the dispersal of weed-seed and grains in this way must have been extremely common.

Mr. Raffill informs me that he once shot a wood-pigeon in winter, the crop of which was full of the rhizomes and underground buds of the Coltsfoot (*Tussilago Farfara*), which were in small pieces, but readily grew. It might be doubted if these portions of rhizome would pass through the intestines in a living state, but some fragments might, or if a hawk or other enemy killed the bird while they were in the crop, they would doubtless grow.

In the Canary Islands a variety of the wood-pigeon occurs which feeds largely on the fruits of *Persea indica* (*Laurineae*), according to Lilford. It probably also eats the berries of the holly, *Ilex perado*, *Hedera canariensis*, and *Myrica Faya*. The bird is also found in the Azores, where the same plants occur.

Columba oenas, the Stock Dove, feeds more among trees and is less frequently to be seen in cornfields, but it is known to eat grain, wheat, buckwheat, and rape. Alice Hibbert Ware (in "The Gizzard Contents of Birds Collected by Miller Christie," *Essex Naturalist*, xx, 142), found the crops of both stock doves and turtle doves full of germinating beans of *Vicia sativa*.

C. livia, Rock Pigeon.—According to Drouet, the Azores variety of this bird eats the fruits of *Persea indica* (*Laurineae*), which is also found in the Canaries and Madeira. It may be this bird which has carried the seeds of the drupaceous

plants common to these islands, from the Canaries to the Azores. F. D. Drewett (in " The Romance of the Apothecaries Garden ") says he found seeds of the Colocynth (*Cucumis colocynthis*), in crops of rock doves in Algeria. This bitter fruit seems to be popular with doves, as there are other records of their feeding on it.

C. fasciata.—Audubon (in " Birds of America, iv., pl. 279) says of this fine large pigeon :—" Swarming flocks were feeding on the berries of the elder tree, and the fruits of *Cornus Nuttallianus*." The drupes of this woodland shrub are oblong and of a bright carmine colour.

Columba arquatrix.—Phillips (in Fruit Dispersal Report, South African Association, xxiv, 425), gives an account of the part played by this pigeon in seed dispersal in South Africa. He gives the following list of fruits eaten by it, of which a considerable proportion of the seeds are passed uninjured: *Podocarpus Thunbergii*, *P. elongata*, *Olea laurifolia*, *O. capensis*, *O. foveolata*, *O. exasperata*, *Elaeodendron croceum*, *E. capense*, *E. Kraussianum*, *Celastrus acuminatus*, *C. peduncularis*, *Pterocelastrus variabilis*, *Olinia cymosa*, *Sideroxylon inerme*, *Ocotea bullata*, *Ekebergia capensis*, *Kiggelaria africana*, *Scolopia Zeyheri*, *S. Mundtii*, *Dovyalis rhamnoides*, *Rhamnus prinoides*, *Scutia Commersonii*, *Halleria lucida*, *Ilex mitis*, *Ochna arborea*, *O. atropurpurea*, *Rhus laevigata*, *R. lucida*, *Euclea lanceolata*, *Royena pubescens*, *Plectronia Mundtii*, *Myrsine melanophloea*, *Rhoicissus capensis*, *Apodytes dimidiata*, *Lachnostylis capensis* (*Euphorbiaceae*) (rarely eaten, but 75 per cent. of seeds pass uninjured), *Virgilia capensis*, and *Curtisia faginea* (*Cornaceae*). The seeds may be carried by this bird for miles. In the case of *Olea laurifolia*, where the tree is abundant, 50 to 100 seeds evacuated by the pigeon are to be found in a square metre, and shot birds contained from 40 to 70 seeds in good germinable condition. He shows also that in many of these seeds passed by these birds, the period of germination is hastened (*Trans. Roy. Soc. South Africa*, xvii., 29).

Columba caribbea in Jamaica feeds on fruits of the Trumpet Tree (*Cecropia peltata*), Wild Raspberries (*Rubus* sp.), Wild Star-apples (*Chrysophyllum olivaeforme*) (*Sapotaceae*), (Gosse).

C. rufina.—Its crop was found to contain the bean-like seeds of madjobitter in Jamaica (Gosse) (*Picramnia antidesma*).

C. leucocephala.—In Jamaica this pigeon ate fruits of Pimento, Sweet-wood (*Laurinea* sp.), Breadfruit (*Brosimum alicastrum*), Burn-wood (*Rhus metopium*), Bastard Cedar (*Guazuma tomentosa*), Figs, *Citharexylon*, Bully-tree (*Sapota sideroxylon*) and Black Mangrove (*Avicennia nitida*) (Gosse). Amadeo (in *Nature*, xxxvii, 535) says that this bird and *C. carensis* have dispersed *Bucida buceras* (*Combretaceae*), *Faramea odoratissima* (*Rubiaceae*), *Solanum stramonifolium*, and *Oreodoxa regia*, into parts of Porto Rico where they did not previously occur.

Carpophaga.—The Fruit Pigeons are great disseminators of the large drupaceous fruits such as Nutmegs, Laurineous and Sapotaceous fruits. They are large, powerful birds, and fly long distances.

Carpophaga Whartoni, of Christmas Island, feeds mainly on the purple black, globose drupe of *Cryptocarya nativitatis*, though it has very little pulp. In this genus the perianth is persistent, and encloses the fruit completely, and is the only eatable part of the fruit. It also eats the orange or purple sweet juicy fruit of *Sideroxylon sundaicum*.

C. concinna.—In Banda the fruit of the true nutmeg is the favourite food of this pigeon, according to Forbes (" Wanderings of a Naturalist," p. 287) and Wallace (" Malay Archipelago," chap. xxix). They state that it devours the mace, the seed or nutmeg being thrown up entire and uninjured. The trees are grown in jungle shade, and attain a height of 60 or 70 feet. The fruit is somewhat like a peach, with a thick, firm, yellowish or creamy pericarp, which splits

along one side and exposes to view the black or dark brown nutmeg in an aril in the form of a crimson network, popularly known in trade as the mace, soft and aromatic.

It is probable that the birds sometimes swallow nutmeg and all, and, digesting the mace, pass the seed by evacuation, as it has long been stated that the Dutch in the eighteenth century attempted to keep the nutmeg in cultivation only in Banda and Amboina, so that they might have control of the market, but their efforts were defeated by the pigeons, who conveyed the seed to other islands. We have no clue as to the length of time which the pigeons habitually retain the nutmegs in the crop before disgorging them, and whether it would allow sufficient time for them to fly to other islands, but most birds which disgorge these seeds (e.g., blackbirds) only take a few minutes to do so. A *Myristicivora*, to which I gave a nutmeg with the mace on, merely pecked off the mace and did not swallow the nutmeg at all. The seed, with the deep brown testa, is about 1 inch long and about as much through, which seems rather large for the *Carpophaga* to pass through its viscera. It seems to be agreed, however, on all hands, that these birds do distribute the seeds to some considerable distance. The tree occurs wild in Ceram, Banda, Amboina, Gilolo and Western New Guinea.

S. Muller (" Reise in den Archipel," ii, 1856, 37) says that *Columba oenea* (*Carpophaga oenea*), and *C. perspicillata*, are the two most famous nutmeg-eaters in Banda ; but there are also *C. viridis*, *C. superba*, and *C. Reinwardtii*. The white Strand Doves, *Columba* (*Myristicivora*, probably) *littoralis* in the Sunda Straits, and *C. luctuosa*, between Celebes and New Guinea, also assist.

Temminck (" Coup d'Oeil," iii, 1849, 294) mentions also *Columba javanica* and *C. diademata* as feeding on nutmegs.

Carpophaga latrans.—In Kew Museum is a specimen of the seed of the Palm (*Oncocarpus vitiensis*) found in the crop of this pigeon.

C. oenea.—Theobald (in Mason's "Burmah," 1860 to 1882) says this bird feeds on wild Nutmeg (*Myristica* sp.), the mace is digested and the seed rejected. The bird always selects the finest fruits, the seeds of which are collected afterwards and used for sowing. Mason says it also feeds on *Ficus* fruits.

C. rhodinolaema.—Hemsley (in " The Voyage of the Challenger") records the following seeds taken from the crops of this bird at the Admiralty Islands :—*Elaecarpus* sp., *Soulamea amara*, *Rubiaceae* (indeterminate), *Myristica* sp., *Laurineae* sp., *Phyllanthus* sp., *Donax* sp., *Gnetum* (2 species). Moseley (" Notes of a Naturalist," p. 386) says :—" Their crops were full of fruits of various " kinds, all of which I had failed to find or reach in the growing state in my " botanical expedition. Among these were abundance of wild nutmegs and " wild coffee-berries. Many of the fruits were entirely uninjured, and the seeds " quite fit for germination. No doubt, when frightened or wounded by " accident, the pigeons eject the whole fruits, and they habitually eject the " hard kernels, as I saw quantities of them lying about under the trees on a small " island on which the birds roost in vast numbers. As soon as a few littoral " trees, such as *Barringtonia* and *Calophyllum inophyllum*, have established them- " selves by their drifting seeds on a freshly-dug coral islet, the fruit pigeons " alight in their branches, in their flight from place to place, and drop the seeds of " all kinds of other trees with succulent fruit. I have seen the pigeons thus " resting on two or three small littoral trees as yet the only vegetation of " Observatory Island, a very small islet in Nares Bay."

Gnetum (perhaps *G. gnemon*) seed has been found in the crop of a pigeon in New Guinea, Guppy also records (*Journ. and Proc. Roy. Soc. N.S. Wales*, xvii, 226) the occurrence of fruits of *Elaeocarpus*, and a Palm, probably *Ptychosperma* or *Kentia*, in the crop of a pigeon in San Christoval, Solomon Isles.

C. perspicillata.—This is one of the nutmeg-eaters as already mentioned.

Wallace ("Malay Archipelago," chap. xxiv), says:—"The Kanary is also "abundant in this forest" (Batchian). "The fleshy outer covering of the nut "is the favourite food of the great green Pigeon, *Carpophaga perspicillata*, "and their hoarse cooing and heavy flutterings among the branches can "almost continually be heard."

Other pigeons of this genus feed on canary-nuts, for Guppy says:—"Both in the Solomon Islands and in the Fijis I am familiar with the dispersal of the "stones of these trees by the fruit pigeons. Stones from the crops of Fijian "pigeons measured 1⅛ inches by 1 inch. In the Solomon Islands these birds "stock the coral islets with trees of this genus, and the ground beneath the "trees is often strewn with the disgorged stones." (Guppy, "Naturalist in the Pacific," p. 400). Temminck ("Coup d'Oeil," iii, 1849, p. 94) states also that pigeons in Banda swallow canary nuts, as do cassowaries and megapodes.

C. novae Zealandiae.—According to Sir W. Lawrie Buller (in "The Birds of New Zealand"), this fine pigeon feeds on a large number of berries and drupes:—*Fuchsia excorticata*, *Solanum nigrum* or *aviculare*, *Hedycarya dentata* (*Monimiaceae*), *Vitex littoralis* (*Verbenaceae*), *Tetranthera calicaris* and *Nesodaphne Tawa* (*Laurineae*), *Entelea arborescens* (*Tiliaceae*), *Myrtus bullata*, *Passiflora tetrandra*, *Elaeocarpus dentatus*, *Schefflera digitata* (*Araliaceae*), *Myrsine australis*, *Alectryon excelsum*, *Santalum Cunninghami*, *Corynocarpus laevigata*, *Cordyline australis*, *C. indivisa*, *Coriaria ruscifolia*, *Podocarpus spicata*, *P. ferruginea* and *P. dacrydioides*, and the hips of the introduced Sweetbriar (*Rosa eglanteria*). This is probably the bird referred to by Ferd. von Mueller as feeding on *Corynocarpus laevigata* in Chatham Island ("Vegetation of Chatham Island").

C. lacerunculata.—A Javanese Fruit Pigeon. Of this, Koorders records that seeds of *Knema laurina*, or *K. glauca* (*Myristicaceae*) were found in its crop.

Phaenorhina Goliath.—Of this fine New Caledonian pigeon, Layard says:— "When the *capsicums* are ripe, these pigeons descend from the mountains to "feed on them." He was much struck by the very large fruits which these birds could swallow. Also *Cormus puniceus*, the Purple-capped Pigeon of Ceylon, used to visit the cinnamon gardens when the fruit was ripe (*Cinnamomum zeylanicum*), and doubtless fed on it.

Treron vernans, the Green Pigeon.—This bird is very common in the Malay Peninsula, and comes in great flocks to the trees of *Ficus benjamina* and *F. retusa* when the fruit is ripe, in the evenings, flying away at dusk to distant roosting-places. They also ate the small brown capsules of *Macaranga robiginosa* (*Euphorbiaceae*). These small rusty brown capsules are borne in fairly large panicles, and are quite conspicuous. The tree occurs in open country. I have also shot this bird feeding on *Rhodamnia trinervia* trees; and the bushes of *Rhodomyrtus tomentosa*, belonging to the same order (*Myrtaceae*), which grow in abundance in open country, and are about 4 feet tall, are constantly haunted by a few. The berry is a small ovoid fruit, turning pink or purplish when ripe, and containing many small seeds. As they ripen, they disappear very rapidly, but to some extent this is due, I believe, to the Turtle Dove (*Turtur tigrinus*). These small green pigeons swallow whole the black round drupes of the Palm (*Oncosperma filamentosa*), which are nearly ½ inch through. According to H. C. Robinson, they are very fond of the fruits of *Melastoma polyanthum*, also an open-country bush, and one of the first bushes to appear in the waste fields of lalang grass, where the seeds are dropped by pigeons and bulbuls.

T. pompadora, the Green Pigeon of Ceylon, feeds on Figs, as do most of the genus.

T. calva, Angola Green Pigeon.—Of this, Monteiro (in "Angola and the River Congo," 164) writes:—"I saw numbers of a beautiful green pigeon "(*Treron calva*). The food of this bird is principally fruit and berries, especially

"the small figs of the Mucoso" (*Ficus brachyphylla* and *F. mucuso* are both called by this name).

Butreron (*Vinago*) *Capellei*.—According to Koorders ("Contrib. to Knowledge of the Flora of Java"), this bird is the main disperser of *Myrica javanica* (*Myricaceae*). One of them had as many as 231 good seeds in its crop. *Myrica javanica* is a medium-sized dark green leaved tree, producing small red drupes. Koorders gives the following note about this plant :—"After the destruction by "fire in Java, 1891, of miles of country, 12 years later the higher slopes of the "volcano, which had been completely burnt, were covered by a forest chiefly "consisting of *Myrica javanica*, and a year after the fire, appeared *Albizzia* "*montana*, growing in groups, the first pioneer of the entirely burnt forest." I have little doubt that the *Albizzias* (a leguminous plant with hard seeds) were derived from old seeds lying in the soil and stimulated to growth by the heat of the fire. The fact that they appeared in groups suggests this also. The genus *Myrica*, the only one in the order, is very widely distributed, and the fruit (in all but the north temperate *M. gale*, the bog myrtle of England) is drupaceous, usually red, and conspicuous. One species, *M. Faya*, is abundant in the Azores, Canaries and Madeira, and has almost certainly been spread there by birds, probably pigeons.

Crocopus phaenicopterus, the Bengal Green Pigeon, and *C. chlorogaster*, the Southern India Green Pigeon, feed almost exclusively on the figs of *Ficus religiosa*, *F. bengalensis* and *F. comosa* (D. D. Cunningham). It is probably the first of these birds that Troup refers to as greedily eating the drupes of *Bridelia retusa*, an Euphorbiaceous shrub with green fruits.

Osmatreron bicincta eats the figs of *Ficus comosa* and *F. religiosa* (Cunningham) in India, and in Ceylon the fruits of *Lantana* and wild dates (*Phoenix* sp.), as well as figs. There are 2 species of *Phoenix* in Ceylon, both very common, *Ph. zeylanica*, with red fruits ½ inch long and ¼ inch through, turning violet-blue, and *Ph. pusilla*, in which the fruits are the same size, but become purple-black (Trimen, Flora of Ceylon).

Sphenocercus Korthalsi, of Java, feeds on the berries of *Gaultheria* and *Eurya japonica* in the mountains of Java (Van Leeuwen).

Macropygia rufipennis.—"Numbers of Blyth's Doves (*Macropygia rufipennis*) "frequented the scrub near the village (Kachal Island, Nicobars), and we were "astonished to find the crops of all those shot completely filled with large "red chillies only" (C. B. Kloss, "Andamans and Nicobars," p. iii). Robinson (in his "Birds of the Malay Peninsula") records *M. ruficeps* also as feeding on chillies *Capsicum annuum*.

Ptilopus porphyreus, the Pink-headed Dove, according to H. O. Forbes, feeds on figs in the Malay Islands.

Chalcophaps indica, the Ground Dove, feeds on berries and seeds picked up from the ground in India (Mason). An almost identical species occurs in Christmas Island, and is probably responsible for some of the plants there. It is always to be seen feeding on the ground in forests in India and the Malay Peninsula.

Turtur tigrinus.—The common Malay Turtle Dove, feeds largely on seeds picked up from the ground, as is the habit of the turtle dove. I have, however, shot them when feeding on the brown capsules of *Macaranga robiginosa*, and noted that their flesh had a bitter taste, perhaps due to feeding on these fruits. It is also common among the bushes of *Rhodomyrtus* in Singapore, and I believe feeds largely on the fruits of this. *T. risorius* and *T. surattensis*, of India, feed mainly on grain and weed seeds. *T. leucopterus*, the Jamaica Turtle Dove, also appears to be usually a seed-eater, but both it and *Chamaepelia passerina* are said by Gosse to eat the seeds of *Jatropha curcas* and *Ricinus communis*, and the pips of the orange in Jamaica, but it may be doubted if any of these are passed in a

good enough condition for germination. *T. capicola*, of South Africa, feeds on and disseminates the fruits of *Ekebergia capensis*, as do *Haplopelia larvata* and *Chalcopelia afra* (Phillips).

Ectopistes migratorius, the Passenger Pigeon, formerly in vast abundance in North America, and occasionally migrating into Europe, is now said to be nearly extinct. V. G. Audubon (in *Canadian Naturalist*, i, 168) states that it fed on buckwheat, hempseed, holly berries, Hackberries (*Celtis*), Huckle-berries (*Vaccinium*), acorns and beech mast. In the crops of some birds, shot hundreds of miles from any rice-fields, fresh rice grains were found. It is clear that this bird must have been a very wide seed-disperser at one time.

Zenaida maculata, in Fernando de Noronha, fed on seeds of *Cassia Tora* and *C. occidentalis*, and probably also on the figs of *Ficus Noronhae*. The crops of those we shot were full of the seeds of the little Wild Melons (*Cayaponia*).

According to Harding King (in " Mysteries of the Libyan Desert ") the Desert Doves feed on seeds (probably grass seeds) and olives. He gives a calculation of the distance and pace they flew at, already referred to. These doves evidently fly from oasis to oasis, and deposit seeds at the damp spots, where they can readily grow. He does not give the scientific name of the doves, but they were probably a species of *Turtur* or some allied bird.

Fruits Dispersed by Various Pigeons of Unknown Species.—*Erythrina* sp. (*Leguminosae*). Alan Cunningham mentions in his diary that he found an *Erythrina* (*E. vespertilio*) in the Dividing Range, Australia, and says : " Its " last year's pods continued hanging on the extremities of the branches, and " though pigeons, which abound in these woods, and other birds, had eaten " most of the seed, still many of a brilliant red colour were found among the " grass beneath each tree."

Dracontomelum vitiense (*Anacardiaceae*). The genus is of rather small spreading trees of tropical Asia, with green drupes, 1½ inches through, with a stone ¾ inch in diameter. Guppy writes of it in the Fiji Islands :—" It is " to the fruit-pigeons that we must look for the dispersal of the genus. In " the crop of one of these birds, shot in Fiji, I found the entire fruit of a " 'Tarawaw tree' (native name)."

Mimusops hexandra, Palu, of Ceylon.—The milky yellow berries of palu are beloved of birds and beasts; hornbills, pigeons and barbets gorge them (Spittal, " Wild Life in Ceylon, p. 62).

Wallace, in the Malay Archipelago, writes that he shot a species of *Carpophaga* much smaller than *C. concinna*, which had a number of globular hard palm-fruits, each more than 1 inch in diameter, in its crop, in the Kei Islands.

Guppy states that he found disgorged seeds of *Canarium* sp., *Ficus* (2 species), *Eugenia*, probably a variety of *E. Jambos* (?), *Litsea*, and 1 species of *Areca*, in the Solomon Isles (Hemsley, " Voyage of Challenger," vol. i, 310).

Couthovia corynocarpa, of Viti (*Loganiaceae*).—The drupes are stated by Seemann to be eaten by fruit pigeons. The stone is from ¾ to 1½ inches long.

Plectronia (*Canthium*) *odorata* (*Rubiaceae*).—Guppy says of this plant :—" In " one locality in Hawaii, where an old lava field was partially covered by its " bushes then in fruit, the doves were feeding greedily on the drupes, the stones " of which, as well as the partially-digested fruits, were to be seen in quantity " in their excrement near a water-hole. The stones are very hard, and about " ⅓ inch (8 mm.) in length." The plant is widely distributed over Hawaii, Tahiti, the Marquesas, and Pitcairn Island. The fruits of this large genus are usually small, yellow or black, from the size of a pea to that of a small gooseberry.

The genus *Canarium* consists of resinous trees (*Burseraceae*), occurring from India to Polynesia, and especially abundant in the Malay Archipelago. The fruits are mostly large, often 2 or 3 inches long, with an extremely hard, stony,

oblong seed, frequently pointed at both ends. The outer covering of the stone is firm, often resinous, with a turpentiny taste, green or, in some of the smaller ones, purplish. The stones, which contain an eatable oily kernel, form the favourite food of the black Cockatoo of Papua (*Microglossa atra*), which can break them sufficiently to extract the kernel, though they are so stony it requires a heavy hammer to break them. They are also sought by the wild tribes (Sakai) of the Malay Peninsula, and I have found in Pahang, in the Malay Peninsula, the ground beneath the trees of an unknown species called Drija strewn with the outer pulp, the stones having been carried off as food supplies by the wild tribes. Their main distribution here, however, must be due to the large birds, hornbills and fruit pigeons.

Elaeocarpus (*Tiliaceae*), are trees with round or oblong drupes, with a hard stone and oily, fleshy pulp, usually green, sometimes purplish, and more rarely bright blue. The green ones are usually disseminated by fruit-bats, but many kinds are swallowed and dispersed by fruit pigeons and parrots. The fruits and their stones vary much in size, sometimes as much as 2 inches in length. Moseley found fruits of a species in the stomach of *Carpophaga rhodinolaema*, as has been mentioned. Guppy noticed that the black fruits of the Toa (*E. Hookerianus*) were the favoured fruit of pigeons in the Solomon Islands, and Hoschstetter and Buller say that the fruits of the Honan (*E. dentatus*) were the favourite food of the parrots and pigeons in New Zealand (Hochstetter, "New Zealand" and "Buller's Birds of New Zealand").

Heisteria coccinea.—The fruit of this plant (*Olacineae*) is stated by Jacquin to be dispersed by pigeons in Martinique. He writes :—"Incolis vocatur "Bois (sive Pois) perdrix, sive arbor sive pisum turturum ob fructus turturibus "amatos" (*Am. Selectae Hist.*, 1788). The *Heisterias* are small trees in which the calyx is accrescent, red or white, forming a large conspicuous ring in which the yellowish or purple (black in *H. coccinea*) drupe appears seated. In this it resembles the allied Malayan genus, *Harmandia*. *H. cyanocarpa* has blue drupes, *H. coccinea* has the calyx lobes distinct in fruit, and the whole calyx is 3 inches across. They are all natives of the West Indies and Brazil.

Cereus giganteus.—Toumey states that pigeons feed on the fruits of the Giant Cactus in the Arizona desert, as well as many other birds, no doubt using it as a water-supply.

Dracaena.—Guppy (in "Plants, Seeds and Currents," p. 488) writes that he found *Dracaena Draco* in Teneriffe growing wild in the Taganana coast. "Here it grows on the faces of rocky declivities in inaccessible parts of the "precipitous slopes of the Roque de las Animas, a pinnacle mountain rising "1,400 or 1,500 feet above the sea. Though growing singly, there were several "trees scattered about on the mountain side in situations suggestive of dispersal "of the seeds. Its station may be compared with that of the Hawaiian *D. aurea*, "which is not uncommon in the wooded districts up to 3,000 feet. Thus "I once found it in the broken-down caverns of an old lava flow frequented by "pigeons, which doubtless brought the seeds. The seeds of *Dracaenas* are "well fitted for withstanding a transport in a bird's stomach, the small embryo "being protected by a very tough albumen."

The *Dracaenas* are very widely distributed over tropical Africa and Asia, and vary from low shrublets to fairly large trees. The berries are red or orange coloured, very conspicuous, and contain from 1 to 3 round seeds.

DIDUNCULIDAE.

Didunculus strigirostris, Samoan Tooth-billed Pigeon.—According to Reinecke the fruits of *Cananga odorata* are sought for by *Didunculus*. The black pulpy berries of this plant, with their hard seeds, did not seem popular with

birds or bats in the Singapore Botanic Gardens, but it was clear that they were occasionally eaten, probably by fruit-bats, as seedlings came up here and there some way from the tree. It is certainly not a native of the Malay Peninsula, but is often planted for its fragrant flowers. Guppy seems to consider it as a native of Fiji and Samoa.

PTEROCLIDAE.—Sand-Grouse.

The Sand-Grouse live mostly in sandy deserts, and, as they have to visit distant pools to obtain water, they can fly immense distances. Most of them are migratory, and some of them wander thousands of miles. They feed on the fruits and seeds of desert plants.

Pallas' Sand-Grouse (*Syrrhaptes paradoxus*) is a native of the Kirghiz steppes and Central Asia, and has at least twice visited Europe in great numbers, once in 1863 and again in 1888, and smaller flocks have been seen in other years. In 1888 it appeared in large flocks between April 21st and May 24th in Poland, Hungary and Prussia, and from May 15th to May 25th from Hampshire to Aberdeen. Mr. Crouch obtained some specimens shot in Essex, and found in their crops some small seeds. They were referred to the author, who identified them as those of *Chenopodium album*, a species of *Carex*, and a few seeds of *Medicago lupulina*. I pointed out that the birds must have brought the seeds to this country with them, for they are not ripe so early in England. Mr. Fitch also examined some of the seeds, and recognised those of *Chenopodium album*, *Polygonum aviculare*, and *Medicago sativa*, and seeds of a species of wild tare which are often noticed in Russian oats. Mr. Fitch also agreed with me that the seeds cannot have ripened in Britain. "It may be noted "that, according to Col. Prjevalski, the principal food of *Syrrhaptes* in its "winter haunts in the Gobi desert, and in Ala-shan, are the seeds of *Agrio-"phyllum gobicum*, a plant allied to *Chenopodium*" (*Essex Naturalist*, 1888, ii, p. 63). Holmboe ("Notizen uber die Endozoischer samen verbreitung der Vogel") states that in the crop of this bird, in Scandinavia, were found seeds of *Polygonum persicaria*, *Chenopodium album*, *Melandrium sylvestre* (*Lychnis diurna*) (doubtful), *Lotus corniculatus*, *Empetrum nigrum*, *Carex*, *Trifolium pratense*, and *Spergula arvensis*. Stevenson (in "Birds of Norfolk") gives the following seeds as having been found in the crops of birds shot in Norfolk:—*Medicago lupulina* and *M. minima*, *Carex* sp., *Rumex* sp., *Stellaria* sp., *Cerastium* sp., *Chenopodium album*, *Polygonum convolvulus*, *Poa annua*, *Sagina procumbens*, *Lepigonum rubrum*.

All these seeds belong rather to the European than the Central Asiatic area. At the same time it must be mentioned that many are widely-diffused species, and probably occur in Central Asia also.

Of the Indian Sand-Grouse (*Pterocles*), Mason records, from various sources, that their food consists almost entirely of hard seeds and berries. *P. exustus* eats especially the seeds of *Alysicarpus*, *Desmodium*, etc.

TETRAONIDAE.—Grouse.

These birds inhabit the mountain forests and moors of the north temperate region in both hemispheres, and feed mainly on the shoots, leaves and berries of Arctic shrubs, chiefly *Vacciniaceae* and *Empetrum*, and are largely responsible for the distribution of these plants over the northern regions. They fly good distances, but apparently never cross any extent of sea, and are absent from all islands.

Tetrao urogallus, the Capercailzie, feeds on berries of Juniper, *Vaccinium oxycoccus* (Cranberry), and *V. uliginosum* (Thompson, in Morris's "British Birds"), to which Birger adds:—*Vaccinium myrtillus* and *V. vitis-idea*, *Melam-*

pyrum sylvaticum or *M. pratense*, *Rubus chamaemorus*, *Carex Goodenovii* and *C. globularis*, and *Calluna vulgaris*, over 100 seeds of the heather being found in one crop. The bird, no doubt, cropped the heather-tops when in fruit and so swallowed the seeds, and might diffuse the heather over large areas.

Lyrurus tetrix, Blackcock.—This feeds on the berries of *Vaccinum oxycoccus*, *V. myrtillus*, *V. vitis-idaea*, *Arctostaphylos uva-ursi*, and *Empetrum nigrum*, according to Thompson. Meyer (" British Birds ") says that where Junipers are abundant it prefers the berries, in the winter, to all other food. It is also reported to feed on the haws of roses, and, according to Holmboe, the fruits of *Rubus saxatilis*, and, according to Ogilvie, eats the berries of the Rowan tree also.

Lagopus scoticus, Red Grouse, is said to feed on the berries of *Vaccinium*, *Arctostaphylos* and *Empetrum*, like the Blackcock, to which it adds achenes of *Eriophorum* and *Carices*, and fruits of *Galium saxatile*, *Rubus chamaemorus*, *Juncus squarrosus* and *Luzula campestris* (flower and seed-heads), *Viola lutea*, and many weed-seeds.

L. lagopus (*L. albus*), the Willow Grouse, feeds on *Vaccinium myrtillus* and *V. oxycoccus*, *Rubus saxatilis*, and *Ranunculus acris* (Holmboe), and in America the fruits of *Maireana* (*Kochia*) *alpina* (*Chenopodiaceae*), *Vaccinium uliginosum*, *V. vitis-idaea*, *Empetrum nigrum* and *Andromeda polifolia*. The fruit of this latter is a dark purple glaucous capsule, but it is probable that the seeds, if swallowed, would pass safely through the bird. *L. subalpinus*, according to Birger, feeds on *Vaccinium myrtillus* and *V. vitis-idaea*. *L. rupestris*, of North America, is reported to feed on the fruits of *Ledum* and *Cassiope* (*Ericaceae*). Both of these have capsular fruit, but the minute seeds may pass through the bird uninjured.

L. hyperboreus.—Ekstam examined a number of crops of this bird in Spitzbergen, and records their contents :—*Saxifraga cernua* (bulbils developing), *Polygonum viviparum* (4,354 bulbils in one bird), *Draba alpina* (fruits), *Cardamine bellidifolia* (seeds), *Cochlearia arctica*, *Cerastium alpinum* (seeds), *Papaver nudicaule* (masses of whole fruit and seeds), *Saxifraga nivalis* and *S. oppositifolia* (fruits and seeds), *Pedicularis hirsuta* (3 ripe fruits in one crop), *Oxyria digyna* (fruits).

L. mutus, the Ptarmigan.—This bird feeds on the berries of the *Vacciniums*, *V. oxycoccos*, *V. myrtillus*, *V. vitis-idaea*, *Arctostaphylos uva-ursi*, *Empetrum nigrum*, and, according to Meyer, eats shoots and flowers of *Erica*, *Calluna* and *Menziesia*. It may swallow and pass seeds of these plants, which all have capsular fruit. H. G. Simmons (in " Survey of the Phytiography of the Arctic America Archipelago ") writes thus :—" *Vaccinium uliginosum* and "*Empetrum nigrum* are sterile in most localities in the North (Arctic America), " though fairly abundant, and are doubtless spread by ptarmigan. It roams " about and burrows in the snow in well-developed vegetation spots, and its " intestines are then well filled with leaves, etc., of *Vaccinium*." Kerner records also the dispersal of bulbils of *Polygonum viviparum* by this bird. F. A. Montague (in " Further Notes on Spitzbergen ") has found in its crop seeds of *Cerastium*, *Draba*, *Oxyria*, Arctic poppy (*Papaver nudicaule*) and grass seeds, and Longstaff has found heads of Arctic poppy and seeds of *Saxifraga oppositifolia* in the crop also, in Spitzbergen.

F. M. Ogilvie records its eating fruits of *Rubus chamaemorus* in Scotland.

Tetrastes bonasia, the Hazel Hen, inhabits Northern Europe and North and Central Asia. It feeds on the fruits of *Rubus saxatilis*, *Empetrum nigrum* and *Vaccinium myrtillus* and *V. vitis-idea*.

Bonasa umbellus, the Ruffed Grouse of North America, eats the fruits of Poison Ivy (*Rhus radicans*), *Lonicera ciliata*, *Rubus triflorus*, R. *villosus*, *Chiogenes borealis*, *Clintonia borealis* (W. S. Durban, *Canadian Naturalist*, iv, 1859, 252).

Pedioecetes phasianellus, the Short-Tailed Grouse or Prairie Chicken of North America, feeds on berries of *Rhus radicans* and Juniper berries. Swinhoe

(in the "Ibis," v) says it eats the fruits of *Arctostaphylos uva-ursi*, *Juniperus prostrata*, *Symphoricarpus racemosus*, *Rosa blanda* and *R. micrantha*, and *Shepherdia argentata*. R. Miller Christy writes that, according to Mr. Thomson, this bird at Carberry, Manitoba, swallows the seeds of *Rosa acicularis* as grit for digestion, as at that spot there are no stones or gravel. It is quite possible that elsewhere other birds pick up hard seeds for this purpose, which may eventually be passed uninjured.

Dendragraphis obscurus, the Blue Grouse of North America, feeds on fruits of *Arctostaphylos uva-ursi* and *A. nevadensis* and *Ribes cereum* (Hart-Merriam in "Birds of Idaho").

Camachites canadensis, the Canada Grouse, feeds on Juniper berries (Phillips), and W. H. Osgood records finding seeds of *Vaccinium* and *Viburnum* in its crop in Alaska.

PHASIANIDAE.—Pheasants and Partridges.

Phasianus colchicus, the common Pheasant, eats largely of acorns, beech-mast and nuts. A. E. Scott (*Country Life*, March 17th, 1928) writes :—"The "cook brought in the contents of the crop of a hen pheasant, killed here (at "Alton, Hampshire, at the end of January). The crop contained 32 sound hazel-"nuts and 4 beech-nuts." They, however, also eat berries and drupes, black-berries, rose fruits and hawthorn berries. Yarrell says they have been observed pulling down ripe blackberries from a hedge, and later in the year flying up into high bushes to pick Sloes (*Prunus spinosa*) and Haws (*Crataegus*). Archibald adds wild cherries, holly berries, yew fruit, and wild rose fruit. Mrs. T. S. Lea informs me that in Norfolk they eat greedily the berries of *Symphoricarpus racemosus*.

In New Zealand G. M. Thomson says that the introduced birds eat largely of the fruits of *Phytolacca decandra*, which cause their flesh to become black.

Polyplectrum chinquis, Grey Peacock Pheasant of India, feeds on the red fruit of a tree with seeds like those of a chilli, and this is used by the natives as a bait for traps for them (Mason). *P. bicalcaratum* eats fruits of figs, Jhamans (*Eugenia* sp.), wild plums, and *Zizyphus jujuba* (E. C. Stuart-Baker, "Game Birds of India," *Bombay Natural History Journal*).

Gallus sp.—It has been recorded that in India Jungle Fowls come in large numbers to feed on the seeds of *Strobilanthes* (*Acanthaceae*), and Lewis, in Ceylon, states that *Stenosiphonium Russellianum* has its seeds eaten by jungle fowl, which, he has no doubt, spread the plant. He also says that other species of *Acanthaceae*, e.g., *Strobilanthes*, are so dispersed. Many of the species in India and Ceylon and Java are gregarious over large areas, forming unbroken sheets of undergrowth. They grow for several years without flowering, reaching a height of 8 or 10 feet, but do not flower for 10 to 13 years, when the whole mass breaks into flower. Then they commence to wither, and ripen the seed, which takes several months or a year, after which the plants die down. It is then, when the seeds are ripe, that the jungle fowl crowd down to feed on them.

I have no record as to whether the seeds occasionally pass unharmed through the fowls, but it is quite possible that wild beasts, panthers and wild-cats may capture and carry off some of the birds, and, in devouring them, scatter the seed. The wild fowls of India (*Gallus bankiva* var.) are fond of all kinds of wild figs and berries (Stuart-Baker).

Gallus bankiva, Domestic Fowl.—There is no doubt that the fowl disperses many small seeds by eating the fruit and passing the seed. Guppy says that in Cocos-Keeling Island they ate the fruits of *Morinda citrifolia* and *Papaya*, and dispersed the seed, and also disseminated *Canna indica*. They are very

largely responsible for the distribution of many herbaceous plants indirectly, being fed with mixed grains and seeds, which, being thrown to them, are not entirely eaten, and so germinate and grow by chicken runs. These are, however, again referred to under " Chicken Food " in " Human Agency," p. 643.

Meleagris gallopavo, the Wild Turkey of North America, is said by Henderson to eat the fruits of *Rhus radicans*.

Pavo cristatus, Indian Pea-fowl.—The Peacock feeds on the fruits of *Zizyphus jujuba*. Their crops may be found full of fruits swallowed whole. They also eat the small dates of *Phoenix acaulis*, which Troup says are a favourite food of this bird. Mason says it eats the figs of *Ficus glomerata* and the fruits of *Carissa carandas*.

Argusianus argus, the Argus Pheasant.—This jungle bird feeds on fruits of *Strychnos* (Jacobson in Robinson and Kloss, " Birds of West Sumatra," *Journ. Fed. Mal. Sta. Mus.*, xi, 202). Hume and Marshall say it lives mainly on fallen fruit, especially one about the size and colour of a prune (Mason).

Gennaeus, the Kalij Pheasants of India, feed largely on berries, as well as dry seeds. Hooker (*Himalayan Journals*, x) writes of one species :—" The " crop was distended with Juniper berries, of which the flesh tasted strongly." *G. melanonotus*, according to Mason, feeds on the fruits of *Rubus flavus* and *Polygonum molle*, two shrubs which yield more bird food in Sikkim than do any other dozen plants put together. Of *G. lineatus*, the Burmese Silver Pheasant, Oates says : " During hot weather pheasants eat the figs of Pipal (*Ficus religiosa*) " ravenously, and I have shot birds with nothing else in their crops."

Ithagenes cruentatus, the Blood Pheasant of the Himalayas, is recorded by Hooker as feeding on Juniper berries. This is confirmed by Jerdon, who says that this food gives the flesh a strong flavour.

Lophura sp., Fire-back Pheasant of Malaya.—Prof. Beebe once showed me a number of crops of these jungle pheasants he had collected in Borneo, which were full of seeds of various kinds. Among them I saw those of a species of *Passiflora* (probably *P. Horsfieldii*, the only wild species there) in some abundance. Unfortunately, time did not permit of my examining the collection more closely.

Tragopan melanocephalus, Indian Horned Pheasant.—According to Mr. Young, quoted by Mason, " its favourite food is the berry of an evergreen " plant called (in Kullu) Deka. I believe it is a species of *Carunda*." (Probably *Carissa carandas*, but the only name like this is applied to *Melia azederach*.) *T. Temminckii*, in China, eats the fruits of *Cotoneaster*, and allied shrubs (E. H. Wilson, " A Naturalist in Western China ").

The partridges and quails which live in open country, cornfields, etc., feed mainly on dry seeds. Whether they pass any of these seeds in condition for germination I have no evidence, but they are very liable to destruction by hawks, stoats, foxes, etc., and birds caught by these enemies may very well be torn to bits and the seeds in the crops scattered. The species living in forests mostly eat berries.

Perdix cinerea, the Partridge, chiefly feeds on dry seeds, but has been known to eat Bilberries (*Vaccinium myrtillus*).

Caccabis saxatilis, the Red-legged Partridge of the Alps, feeds on Juniper berries (S. B. Wilson, " Ibis," 887, p. 150).

Ammoperdix Cholmleyi.—" The isabelline gazelle had been feeding on the " smaller red berries of a kind of *Berberis*, on which we noticed that Cholmley's " Sand-Partridge (*Ammoperdix Cholmleyi*) also feeds " (A. Chapman, " Savage Sudan "). This was doubtless *Berberis Forskaliana*, the only species recorded in the Eastern Sudan.

Arborophila Campbellii, the Tree Partridge of the Malay Peninsula,

according to H. C. Robinson, finds in the small red berry of the creeping *Pratia begoniaefolia* (*Lobeliaceae*) its favourite food.

Galloperdix spadicea, Indian Red Spur Fowl, eats the fruit of the dwarf *Zizyphus nummularia* (Jahrberi) and figs of *Ficus religiosa* and other species (Mason). *G. bicalcarata*, the Ceylon Spur Fowl, feeds on the berries of *Lantana* (Stuart Baker).

Coturnix communis, Common Quail, feeds largely on dry seeds. It has been recorded that 3,500 seeds of *Stellaria media* have been found in the crop of one bird. It also eats fruits of *Atriplex patula*, *Plantago*, *Rumex* and Vetches. Pistone adds the fruits of *Phytolacca decandra*. In India it eats, besides grain and pulse, small berries like those of *Zizyphus*.

Coturnix australis, the Australian Swamp Quail, was introduced into New Zealand, where, according to M. M. MaKai, "they are most active "agents in the spread of blackberries and gorse in Auckland." *C. pectoralis*, of New South Wales, eats occasionally fruits of *Solanum nigrum* and *Phytolacca decandra*, besides achenes of *Ranunculus*, and seeds of *Stellaria media* (Thomson).

Francolinus vulgaris, Black Partridge of India.—Mason has found seed of *Ficus* sp. in the crops.

Calloperdix oculea, Indian Wood Partridge, feeds on figs (Stuart-Baker).

The greater number of the *Phasianidae* subsist mainly on dry grains, seeds of herbaceous plants, acorns and such fruits and seeds, but it is possible that they may pass some of these uninjured, and all of the birds are very liable to destruction by eagles, falcons, foxes, stoats, wild-cats and such enemies, by which the contents of the crops might be scattered. However, nearly all sometimes feed also on berries and drupes. They are mainly continental birds, not crossing the sea, but the quails and some of the smaller *Perdicinae* are migrants. Both the common quail and Red-legged Partridge (*Caccabis rufa*), are found in the Azores, but are possibly introduced.

CRACIDAE.—Curassows.

Crax alector feeds on the Sapodilla fruits, *Achras sapota*, in South America (Huth).

Penelope cristata.—"I remember coming on a flock of one of the small "Turkeys called Cuyubi (*Penelope cristata* or an allied species) on the banks of "the Uaupes, feeding on the fruit of so deadly a plant as a Strychnos (*S. rondele-*"*tioides*), but the succulent envelope of the fruit is innocuous, like that of our "poisonous Yew" (Spruce in "Notes of a Botanist," ii, 377). He also refers to *S. braziliensis* having red 3-seeded fruits, whereof the pulp is edible though insipid (l.c., i, 164). (Most of the Malayan species of *Strychnos* have berries of various sizes, some small and yellow, strongly bitter with brucine. Monkeys and civets certainly eat the larger fruits, and probably birds eat the ones with small yellow berries.) "On the slopes of the volcano Tunguragua, of the "Quitonian Andes, I have seen flocks of another turkey feeding on the plum-"like drupes of the Motilon" (this name is given to *Symplocos cernua* and also to two or more species of *Hieronyma*, all bearing edible drupes) "and on the "berries of an undescribed *Melastome*. Besides these fruit trees, there were "also numerous fruit-bearing bushes near, including some true brambles, "whortleberries, and a hawthorn, all of which probably afforded food to the "turkeys" (Spruce, l.c., ii, 378).

Oreophasis derbianus.—Salvin ("Ibis," ii, 251) writes that he found this Guatemalan bird eating the fruit of a fine forest tree, a *Prunus* closely allied to *P. occidentalis* of the West Indies.

TINAMIDAE.—TINAMUS.

These are partridge-like birds of South America. G. Claraz says that *Nothura maculosa* feeds on the white berries of the heath-like shrub *Margaricarpus setosus*, which is hence called *Yerba de perdiz* by the Spaniards. The plant occurs widely distributed over temperate South America and in Juan Fernandez.

MEGAPODIDAE.—MEGAPODES.

The Brush Turkeys eat a certain amount of fruit. *Megapodius Forsteni* and *M. rufipes* of Ceram, according to Temminck (" Coup d'Oeil," iii, 1849, 294), live on cloves, nutmegs and canary-nuts (*Canarium*).

RATITAE.

The ostriches, emu and cassowaries, being wingless, cannot disperse seeds across very large stretches of water, though cassowaries are known to be able to swim for a considerable distance; but they undoubtedly can, and do spread plants by seed over the large areas which they inhabit in the same way as terrestrial mammals do.

Casuarius, the Cassowary, lives on fruits, and can swallow very large stones, 2 inches through and more, and pass them in their excreta. Guppy (" Naturalist in the Pacific," p. 152) states that a cassowary kept in Cocos-Keeling Island was a very efficient distributor of the seeds of *Ochrosia parviflora* (*Apocynaceae*), scattering the undigested seeds everywhere, and causing the young trees to become so numerous that they had to be destroyed. Beccari states that the cassowary of the Aru Islands swallows the fruits of *Orania aruensis* (*Palmaceae*), which are 2½ inches through, and so disseminates the Palm. S. Müller (in " Reisen in den Indischen Archipel," ii, 1856, p. 37) states that the cassowary of Ceram (*Casuarius galeatus*), swallows nutmegs, and Temminck (" Coup d'Oeil," iii, 1849, p. 294) confirms this, and adds that it also swallows the fruits of *Canarium*.

Struthio camelus, Ostrich.—Mr. Burtt-Davy gives an account of the food of the ostrich (in the *Transvaal Agric. Journ.*, vii, 49). He gives a list of about 22 plants, chiefly herbaceous ones. Of these, 7 are *Compositae*—*Pentzia virgata*, *Aster filifolius*, *Felicia procumbens*, *Phymospermum parvifolium*, *Arctotis calendulacea*, *Sanchonanthus camphoratus*, *Chrysocoma tenuifolia*. The achenes of these are hardly likely to pass through the bird unharmed, but those of the following plants might readily be dispersed by it:—*Mesembryanthemum* spp., *Galenia spathulata* (capsule fleshy), (*Ficoideae*), *Walafrida geniculata* (*Verbenaceae*), *Monechma divaricata*, *Justicia* (*Acanthaceae*), *Hermannia pallens* (*Sterculiaceae*), *Grewia cana* (*Tiliaceae*), *Cassia tomentosa*, *Acacia horrida*, *Lycium austrinum* (*Solanaceae*), *Atriplex capensis*, *Caroxylon aphyllum*, *Salsola glabrescens*, *Lepidium capense*, *Portulacaria afra*.

In the Kalahari desert it eats the Wild Melons (*Cucumis melo*) and small forms of the Water Melon (*Citrullus vulgaris*). Livingstone (in his " Missionary Travels ") also mentions its eating the wild melons in the Kalahari desert, and adds fruits of the *Leguminosae*.

Dromaeus Novae-Hollandiae, the Emu, cannot swallow the large stones which the cassowary requires to keep it in health; and, indeed, the fruits of Australia, where it lives, are not so large as those of Papua and Ceram, the home of the cassowaries. It is stated by W. B. Alexander (in " Prickly Pears Naturalised in Australia ") that it is one of the disseminators of the *Opuntias*, *Nopaleas* and other Cacti now running wild in Australia. J. W. Audas (in " One of

Nature's Wonderlands," p. 67) writes :—" Several emus were feeding on the " berries of these heaths, *Astroloma humifusum* (Cranberry heath), *A. pinifolium* " (Pine heath), and *A. conostephioides*, Flame heath (*Epacrideae*)," and also mentions (p. 95) these birds feeding on *Styphelia ascendens*, a low semi-shrub producing large green, oval, sweet berries, much sought after by emus.

Rhea sp., the American Ostriches, eat fruit to some extent. Cunningham (in the "Natural History of the Magellan Straits") states that the berries of *Empetrum rubrum* are eaten by ostriches as well as by geese.

Apteryx Bulleri.—Buller says that this Kiwi eats the fruits of *Elaeocarpus dentatus* and *E. Hookeri*, of *Santalum Cunninghami* and *Podocarpus ferrugineus*. It seems to swallow the harder seeds in place of stones, to assist in digesting its food. Though all the Kiwis live mainly on worms and insects, most occasionally eat berries or drupes as well.

PART VII

BIRDS' NESTS

Birds, in collecting material for the construction of their nests, frequently carry branches of herbs or shrubs, and panicles of grass with attached seeds, to the place selected by them, or may carry plumed seed to line the nests, or portions of living plants, which may continue to grow. In cases where (in the Antarctic regions especially) the sea-birds make their nests in the grass tussocks, the grass seeds may become embedded in their down and so get borne away. This latter method of dispersal, however, I deal with under "Adhesion to Birds," pp. 556, 557, 561, 589.

In some cases the pieces of plant or plumed seeds may be carried from a considerable distance, and it is probable that many of the plants found growing in the tops of pollard willows have been brought there in this way (*see* Epiphytes, p. 30). Some of the more readily attached seeds or fruits may be carried to the nest, and eventually, by adhesion to the bird, be later carried farther away in its more distant flights (e.g., *Galium aparine*). The seeds of berries or drupes brought to the nest for the food of the young birds may be deposited in or about the nest. I have seen a considerable number of seeds of the ivy in an old robin's nest. The nest, when abandoned, breaks up, and the bits are drifted away by wind and rain, and so spread the seed further.

Harting (in "Sketches of Bird Life") says that the garden warbler always makes its nest from pieces of *Galium aparine*, and no doubt in this way spreads the plant from one hedge to another. Meyer states that the white-throat and Dartford warbler use the same plant. Common sparrows (*Passer domesticus*), and probably many other birds, carry grasses and other scraps of vegetation, often bearing seeds, to their nests from some distance, and in doing so frequently let them fall in the neighbourhood of the nest, or on the way to it, so that seeds may be dispersed in that manner. Sparrows seem to do this all the summer. I find them in June collecting pieces of new-mown hay to repair the nests, below which I have found panicles of *Poa pratensis*, *Trisetum flavescens*, and *Luzula campestris*, all containing ripe seeds. In the autumn I have seen them every year gathering pieces of the fruiting panicles of *Cortaderia argentea*, the Pampas Grass, for their nests, 50 yards away. Meyer says that the wood-wrens also use panicles of grasses in building their nests.

Willis and Burkill (in Cambridge Phil. Soc., viii, 2) give the following seeds as found in birds' nests :—

Thrush.—*Galium aparine* (13 fruits), *Poa annua*, *P. pratensis*, *Bromus sterilis*, *Lamium purpureum* (a living plant), *Dactylis glomerata* (a live plant).

Sparrow.—*Carduus* sp., *Phragmites communis*, *Poa* (3 species), *Lolium*, *Bromus mollis*, *Deschampsia caespitosa*, *Festuca ovina*, *Dactylis glomerata*, *Agropyrum*, *Alisma Plantago*. In one sparrow's nest was a fresh piece of *Elodea canadensis*.

Wren.—*Daucus carota* and *Galium aparine*.

S. Birger examined a number of birds' nests in the Swedish islands, and found the following plants utilised by the birds :—

Sterna hirundo, Common Tern.—Root-stocks of *Phragmites*, *Solanum dulcamara*, *Elodea canadensis*.

Podiceps sp., Grebe.—This bird used mosses chiefly, but also *Phragmites* and *Agrostis stolonifera*.

Larus canus, Common Gull.—Twigs and roots of *Solanum dulcamara*.

Anas boschas, Wild Duck.—In its nest were ripe seeds of *Salix cinerea*.

J. R. Matthews (in a paper on the " Dispersal of *Zannichellia palustris*," Trans. Perth Soc., viii, p. 74, 1920), says :—" Growing over an old nest " of a water-hen in Keltie Lock, Perthshire, were *Cerastium vulgatum* and *Galium* " *saxatile*. These two plants had almost certainly been introduced with pieces of " dead twigs of gorse gathered from the hillside by water-hens." On the high chalk cliffs of Ballard Down, Swanage Bay, can be seen from the sea a considerable clump of *Erica cinerea* about halfway up the chalk face, which has certainly been there for several years. It is quite inaccessible, and can only be seen from the sea. Small plants of the *Erica* can be found in the north side of this Down, but none on the centre and south face, where this clump is to be seen. The nearest point at which the plant is large and abundant is on the Studland Heath, 2 miles away. This chalk cliff is inhabited by gulls, cormorants, and jackdaws, which nest in depressions or holes in the face of the cliff. Jackdaws are well known to bring large quantities of twigs to build their nests, and the only way I can account for its presence here is that a jackdaw brought a branch of this plant carrying seeds, to its nest on the cliff, and they grew there. The seeds of *Erica* often remain undistributed from the plant till well into the spring, when the bird would be nesting.

In Christmas Island the Boobies (*Sula piscator*) carried pieces of the succulent herb *Sesuvium portulacastrum* to their nests. These portions may very readily grow, and I believe this widely-distributed plant owes much of its dispersal to this use of it by sea-birds.

E. Chilton (in the " Sub-Antarctic Islands of New Zealand," *Ecology*) writes that he found *Stellaria decipiens* and *Luzula crinita* growing on the nest of the albatross in New Zealand. The young albatross has much to do with the spreading of *Acaena*, since the fruits are attached to their breasts in great quantity, and they do not fly from the nesting-place, but walk over the meadows to the sea. Chapman (in Trans. New Zealand Inst., xxxiii, 516) confirms this adhesion of fruits of *Acaena ascendens* in abundance to the breasts of young albatrosses. These birds make their nests in tussocks of *Spartina*, etc., and the grains of these and other grasses amongst which they nest doubtless become embedded in the down of the under-surfaces, and are carried away to distant islands by them, and with them also the seeds of the small herbaceous plants which may be stuck by mud on their feathers and feet. These nest-contents are probably the origin of the greater part of the vegetation of the Antarctic islands.

Schimper (in "Die epiphytischen Vegetation Amerikas") says birds frequently use the strands of *Tillandsia usneoides* for building their nests, and in South Brazil, C. Dixon (in " Birds' Nests ") says that *Ostrinops decumanus* builds its nest of this plant, and, as any piece of this plant will grow, it is readily spread by the birds.

Schenk, in the " Dissemination of *Usnea barbata*," says that though this lichen is mainly dispersed by wind, he has seen birds building their nests with it, the lichen being in good growing condition. It is extremely probable that it is so dispersed by birds.

The plumed and woolly seeds of plants are often used by birds to line their nests. In the Museum at Kew is a large nest of the White-Collared Swift of Trinidad, made of the plumed seeds of *Catopsis nutans* (*Bromeliaceae*). The nest of *Elainea Ridleyana*, the Tyrant Bird of Fernando de Noronha, was thickly lined with, or almost entirely made of, the plumed seeds of *Gonolobus micranthus* (*Asclepiadaceae*). Monteiro (in "Ibis," iv) states that the Bee-Eater (*Merops Savignii*), in Africa, lines its nest with the woolly seeds of *Cochlospermum angolense* (*Bixaceae*). These woolly seeds collected by the birds for their nests may well owe some of their dispersal to this system.

CHAPTER V

DISPERSAL BY REPTILES, BATRACHIANS, FISH, INSECTS, ETC.

Reptiles and Batrachians as Seed Dispersers—Dispersal by Fish—Dispersal by Insects, The *Elaiosome*—Dispersal by Crustaceae—Snail Dispersal—Dispersal by Earthworms.

REPTILES AND BATRACHIANS AS SEED DISPERSERS.

THE reptiles of the present era are chiefly carnivorous, but some occasionally (or even regularly) feed on fruits, and disseminate them. In the Mesozoic era, when reptiles attained their greatest development, many were plant-feeders, and may have been responsible for a greater seed dispersal.

Lizards.—Guppy (in " Plants, Seeds, and Currents," 487) describes how Iguanas in Long Cay and Greater Sand Cay, Turk's Islands, West Indies, transport the seeds of *Genipa* (*Rubiaceae*). The fruits of *Genipa clusiifolia* are evidently appreciated by these animals, and it is remarkable that the two islands frequented by them are just those where the Seven-Year Apple (*G. clusiifolia*) grows in greatest quantity.

W. Beebe (in " Galapagos," 250) says of the big land Iguana (*Conolophus subcristatus*) :—" One had swallowed whole, 5 cactus fruits, and another 3. " That these lizards are agents in the dissemination of plants was everywhere " evident. Wherever old droppings of *Conolophus* lay on a beach or veldt, " there a colony of seedlings was growing strongly " (p. 251). Darwin describes this lizard as feeding on *Acacia*, and Beebe saw it feeding in a *Maytenus* tree. It seems to be mainly vegetivorous. Iguanas and alligators are said to eat the Alligator Apple, *Anona palustris* (Guppy). John Beattie (*Journ. Zool. Soc.*, 1926, p. 31) states that the stomach of a Teguexin Lizard (*Tupinamba*) contained numerous dark brown seeds only. P. C. Standley (in " Trees and Shrubs of Mexico," Contrib. U.S.A. Nat. Herb., xxiii, 202, 1922) says that the fruit of *Celtis iguanea* is eaten by iguanas in Mexico. Hence the scientific name. The fruit is a small sweet drupe.

Tortoises.—Stewart, in the account of the Galapagos Tortoises, states that their food consists of the succulent green stems and fruits of the Cacti, and that those round Cape Rose, Albemarle Island, ate the fruit of *Hippomane mancinella* (the Manchineel tree) in great quantity. The fruit resembles a small yellow apple. It is always considered to be very poisonous, and Stewart says that the diet had weakened the tissues of the alimentary canal very greatly. I have already recorded Sloane's statement that the goats in Jamaica ate it and dispersed the seeds (*see* p. 369). It seems extraordinary that these animals should devour such poisonous fruits with such impunity, and that though it has a deleterious effect on the alimentary canal, they should survive long enough to grow up and reproduce their species, though they have not completely immunised themselves from the action of the poison.

Darwin (in " the Voyage of a Naturalist ") writes of them that those which live on the islands where there is no water, or in the lower and arid parts,

eat chiefly of the *Cactus*. Those which frequent the higher or damp regions eat leaves, and the fruit of a berry called *Guava vita* (I suppose this to be the fruit of *Psidium galapagoense*, a kind of wild guava).

Batrachians.—These animals, being insectivorous, play but little part in dispersal of plants. Their action in diffusing such floating plants as *Lemna*, *Wolfia* and *Azolla*, is dealt with under Transportation by Birds, etc., of portions of living plants (*see* p. 356). Toads, however, appear to play an indirect part in the dispersal of fungi. Germinating spores of a species of *Russula* and *Lactarius* have been found in their viscera from slugs which they had eaten and which had themselves previously fed on the fungi. The old name of Toad-stools for the *Agarics* is, therefore, perhaps not quite a misnomer.

DISPERSAL BY FISH.

A large number of freshwater fish are vegetable feeders, and may often swallow the seeds of water plants and of plants growing on the banks of rivers and pools. In the Botanic Gardens of Singapore I have seen numbers of Cat-fish (*Clarius magur*) feeding on the figs of *Ficus Benjamina* as they fell into the water. In such cases, however, the excreta would be passed in the water and the seeds of such plants doubtless wasted. Fish, however, frequently feed on the fruits of plants which are of an aquatic habit, and may convey the seeds swallowed by them to different parts of a river or to distant branches, or even from one river to another by passing some distance through the sea.

Many fish also have the power of passing from one piece of water to another overland, usually through wet grass, the passage being almost invariably made by night, when the grass is wet with dew, if not with rain. In the Malay Peninsula it was far from uncommon to find fish in wells and such isolated pieces of water, which they must have reached by passing over land. Thus I have seen catfish in wells, where they must have crept by themselves.

Migrating fish of such kinds are Malay Catfish (*Clarius magur*), the so-called climbing Perch (*Anabas scandens*), and eels (*Monopterus javanicus*). Other fish probably migrate short distances over land. Many years ago I had some small eels in a pan of water near Aber, North Wales. They remained there quietly till one evening they jumped out of the pan. They were replaced, but after dark a violent storm of rain came on, and next morning they were found to have escaped and had gone back to the sea, which was many yards away.

Fish, by going up very small streams, can readily, in some places, pass from river to river, and may thus convey seeds which they have swallowed.

The large artificial lake in Singapore Botanic Gardens was supplied by a stream from another pond, the water of which was derived from springs. No fish were ever, so far as I could gather, put into the lake, yet it abounded in fish of 8 or 9 kinds, which may have been responsible, to some extent, for the appearance of the aquatic plants there.

Among the plants probably dispersed by fish I would mention *Pandanus helicopus*, which grows so abundantly in the Peninsula and in Sumatra that it has a tendency to choke up the rivers. Fish are so fond of this fruit that the Malays use it to bait fish traps. The drupes, which form a large head, are small enough to be swallowed by even a small fish. Fish also feed on Water-lilies, and when I threw a segment of the fruit of *Nuphar lutea* into a tank in Kew Gardens, a carp rose and took it at once, rejecting the firm outer coat and swallowing the pulp and seeds.

P. Luther (Medd. Soc. Faun. and Flor., Helsingfors, 1901, p. 76, " Samenbreitung bei *Nuphar luteum* ") states that a specimen of the fish, *Scardinius*

erythropthalmus, the Rudd, was caught in the Logo Sea, in Finland, which had the intestines full of the seed and flesh of *Nuphar luteum*. The seeds were washed and planted. Of 39, 3 had germinated in 15 days, the next day another one germinated, but the rest had not germinated in 4 months. Of 81 seeds taken direct from the *fruit*, as a control example, none had germinated within that period, and he suggests that the digestion of the fish had improved the germinating capacity of the seeds.

G. Hochreutiner (*Bull. Herb. Boiss*, 1899, p. 450, in "Dissemination des Graines par les poissons") gives an account of some experiments he made. He fed the seeds of *Menyanthes trifoliata* to the Roach (*Leuciscus rutilus*), the Goldfish (*Cyprinus auratus*), and the Perch (*Perca fluviatilis*). The fish retained them in their viscera for 1 or 1½ days, 3 days, and 1 day respectively. The seeds, when passed, nearly all germinated. The fruits of *Sparganium simplex* given to the roach, and *Gunnera chilensis* to the goldfish, when passed, failed to germinate. Seeds of *Nymphaea coerulea* fed to perch were retained in the viscera for 1½ days, and of 20, 11 germinated after evacuation. Of *Sagittaria sagittifolia*, of 6 seeds swallowed by a roach and retained for 2 days, 4 out of 6 germinated. Of *Alisma plantago* fed to roach, 20 out of 80 evacuated seeds germinated. Seeds of *Potamogeton polygonifolius* fed to roach, and passed after 2 days, failed to germinate, but fed to perch, 2 germinated after 1½ days.

Dispersal by fish can be effected in another way, as was shown by Darwin (in "Origin of the Species," chap. xii). He forced many kinds of seeds into the stomachs of dead fish and gave their bodies to fishing eagles, storks and pelicans. These birds, after an interval of many hours, either rejected the seeds in pellets or passed them in their excreta, and several of these seeds retained the power of germination. Certain seeds, however, were always killed by this process. "Even small fish swallow seeds of moderate size, as those of the yellow "water-lily and *Potamogeton*. Herons and other birds, century after century, "have gone on devouring fish daily; they then take flight and go to other "waters, or are blown across the sea, and we have seen that the seeds retain their "power of germination when rejected many hours afterwards in pellets or "their excrement." He then quotes Audubon's statement that he found the seeds of the great yellow Water-lily (probably *Nelumbium luteum*) in a heron's stomach (*see* p. 494). "Now, this bird must have flown, with its stomach "thus well stocked, to distant ponds, and analogy makes me believe that it "would have rejected the seeds in a pellet in a fit state for germination." Birds, such as herons, storks and pelicans, fly for very great distances to reach water. They are constantly moving about. The little blue heron was frequently seen on Christmas Island, where it must have flown from Java, a distance of 194 miles.

A white-tailed Fishing Eagle (*Haliaetus leucogaster*) at one time nested in the Garden Jungle in Singapore, 4 miles from the sea. It brought food for its young every day to the nest, and I have picked up a cuttlefish bone, which it had brought, at the foot of the tree.

It is, however, more probable that the heron family is the main disperser of fish-swallowed seeds, as the sea-eagles feeding on sea fish would not be likely to bring seeds of plants that would grow inland, in this way to their nests.

J. Ruggles Gates (in a "Botanist on the Amazons," p. 129), writes of the Mungubeira (*Bombax Mungubu*):—"The Prelate says the seeds are eaten by "fish. When a seed and fluff falls into the water, a fish rises and takes it." The tree grows on the banks of the river, and the fluffy seeds are, no doubt, mainly dispersed by wind, but the fish may carry them from river to river, or up stream.

A. Piccone (in the "Disseminazione dei Alghe") gives an account of investigations into the food material found in marine fishes, especially *Box Salpa* and *Sargus Rondeletii*, in which he shows that they eat largely of marine algae, *Zostera* and *Posidonia*. The marine algae devoured by these fish were found in many cases to be fruit-bearing, and it is probable that the algae may be dispersed by the fish. He only found leaves, or portions of leaves, of *Posidonia* and *Zostera* in the intestines.

DISPERSAL OF SEEDS BY INSECTS.

Insects play a comparatively small part in the dispersal of seeds, but in some cases a rather important one. There are three ways in which they disseminate seeds and spores—by swallowing them and passing them in their excreta, by carrying them to their nests for the purpose of eating the caruncle or oil body (Elaiosome), and by the adhesion of spores (and possibly seeds) to their bodies.

The first case is rare (except in the case of fungus spores). Darwin, however, gives an account of the carriage of seeds by locusts in Natal ("Origin of Species," chap. xii). He states that the farmers believed that injurious seeds had been introduced into their grass-land by locusts, which passed them through their dung, and, having obtained from Mr. Weale a small packet of the dry pellets, he raised from it 7 grass plants of 2 species of 2 genera. As the locusts fly very long distances (he mentions catching one 370 miles from the coast of Africa), it is quite possible that these insects might convey very small seeds in this manner to very great distances. It is commonly stated that, after an invasion of locusts, weeds spring up not known before in the devasted area. Further research on this means of dissemination is much wanted.

Termites (*Neuroptera*).—The white ants, or termites, seem to play but little part in transportation of seeds of flowering plants, but do carry about the spores and sclerotia of fungi to their nests to cultivate them for the young, which in many cases are fed exclusively on sclerotia of some species of Agaric, cultivated by them in their fungus gardens. Mr. Burtt-Davy, however, tells me that in the Transvaal the remarkable grass *Cynodon incurvatus* is distributed by termites in the following manner :—"These insects collect fragments of the "grass and its seeds, and store them in the upper chambers of the nest. After "the nest is broken down by the attacks of the Aardvark (*Orycteropus*) or other "destructive animals, the seeds germinate and produce a patch of the "grass." This grass only occurs in open spots, pathways, etc., in the veldt, being, from its low growth, unable to compete with the taller grasses, so that it chiefly occurs on the bare sites of the destroyed nests, covering them with a dense mat. P. Th. Justensen (in "Morphological and Biological Notes on *Rafflesia*," *Ann. Bot. Buitenz.*, xxxii, 64) suggests that termites may play some part in the dispersal of the seeds of *Rafflesia*, by invading the fruit at the base and entering the ovary (where he has found them), and emptying the ovary of seeds, much as, I understand, they do in attacking the fruits of *Dillenia* (*see under* Rain-Wash, p. 168). "The seeds thus dislodged by the termites might "then be diffused by the activity of digging or termite-eating mammals, which "might carry the seed on their feet or in their bowels. We might think of the "wild pigs, pangolins, or mice."

Termites are well known to carry off spores of fungi to cultivate in gardens made of their excreta, to feed the young ones on. There is a considerable amount of literature on the subject, which is detailed by Mr. Petch (in *Ann. Bot. Gard. Perad.*, iii). He shows that the fungi cultivated by them in Ceylon are a white

Agaric, *Volvaria eurhiza*, *Xylaria nigripes*, and *Entoloma microcarpum*. I have frequently seen a white agaric, resembling his figure and account of the *Volvaria*, on the deserted nests of termites in Singapore. The termites seem to collect decayed wood with mycelium of one or other of these fungi, and devour it, forming their curious gardens of the excreta, on which grow the sclerotia which supply food for the young termites. After the termites have swarmed and the nest is abandoned, the pilei develop from the mycelium.

Dissemination by Ants.—It is, however, amongst ants that we find the most important seed-dispersers, and the story of these insects and the part they play in the dissemination of seeds of herbaceous plants has been the subject of study of many naturalists. There are two reasons for the action of ants in seed-transport. Certain species have the habit of carrying off seeds, chiefly of grasses, to their burrows, and storing them up for food, usually eating off the plumule and radicle when they germinate, or biting them to bits. In this case a large proportion of the seeds are actually destroyed. I have often, at Singapore, seen piles of bitten-up grass seeds thrown out of their nests, of which all were ruined for germination purposes. But it appears that frequently, in their transport, they drop the seeds here and there *en route*, and so spread the species, and again the nest may be dug up or accidentally destroyed and the seed-store scattered. Certain ants, too, build their nests of bits of stick, etc., and often carry seeds to utilise in the structure. The common Wood-Ant (*Formica rufa*) of the pine woods does this, and so transports seeds from one place to another. More important, however, is the transport of seeds by ants for feeding on the *Elaiosome*, or oil-body, or on oil exuded by the testa of the seed. This oily substance is very attractive to ants, and they seek for seeds and fruits so furnished, and carry them to the nest, very frequently eating off the oil-body on the way and then dropping the seed. In these cases the seed itself is not eaten or injured, so that, even if it is carried to the nest, it may soon germinate and grow there.

The transport of seeds by these insects is not, of course, to any great distance, but it certainly adds a good deal to the diffusion of plants in the locality, and it is probably of considerable importance in the matter of dispersal of epiphytic plants in the tropics, as they carry them from tree to tree, or branch to branch, and plant them in suitable spots. The general importance of ants in relation to plants I have described in my paper of "Ants and Plants" in the *Annals of Botany*.

Ants seem to reach oceanic islands very readily, probably in floating logs, nests and all. In these cases seeds collected by them and stored in the nests may in this way reach the islands, and this may account for the appearance of the small-seeded grasses and herbaceous plants on islands.

I describe first the use of the *Elaiosome*, as it is really the most important factor in ant-dissemination, and it will be noticed, in the account of transport of seeds by ants, that some of them possess oil-bodies or oil-glands, and others are taken as food themselves. The general subject is treated of according to countries. We have very little information as regards the tropics, however. There are probably further notes published in the extensive publications on entomology which I have not been able to trace, but the accounts I have been able to procure give a good idea of the useful work of these little creatures.

The Elaiosome.—Perhaps the most important and extensive paper on this subject is one by Sernander, entitled "Entwurf einer monographie der Europaischer Myrmekochoren" (*Kungl. Svenska Vetenskap Akademiens Handlingar*, 41, vii, 1906). Like many other botanists, he uses the term "*Myrmekochore*" for a plant whose seeds are dispersed by ants. I see no advantage to be gained by forming and using words of this nature, therefore I have excluded all such

confusing and unnecessary terms. Sernander shows that the part of the seed, fruit, or flower which is attractive to ants, and induces them to carry off the seeds to (or part of the way to) their nests, varies in different groups of plants, and calls this part the *Elaiosome*, or oil-body, as it usually contains an oil, a foodstuff of the ants, which eat it after carrying the seed off and leave the seed or fruit at some distance from the parent plant. In some plants the oil only occurs in the seed-coat, and is licked off by the ants, in others the oil-body consists of the funicle, strophiole or caruncle, the base of the pericarp, or, in the case of nutlets, a portion of the floral axis (receptacle), or, in *Carex*, the base of the utricle, or in some plants a part of the inflorescence is the attraction.

He divides the species so dispersed into 11 types, according to the parts containing the oil and forming the *Elaiosome*, and I give his sections or types below. The *Elaiosome* really plays the same part to the ants as does the aril to birds, and in many cases is actually the same structure. The seeds are dropped on the ground from the capsule (in rare cases the ants ascend the plant and gather the seed, as will be seen), and are picked up by the ants and conveyed to the nest, the insects often nibbling off the *Elaiosome* as they go, and dropping the uninjured seed.

1. *Puschkinia* type.—These have no *Elaiosome* at all, but the seed-coat contains a quantity of oil which is attractive to the ants. These are mostly *Liliaceae*. Among them are *Allium ursinum*, *Ornithogalum Kotschyanum*, *O. nutans*, *Puschkinia scilloides*, *Triteleia uniflora*, etc.

2. *Viola odorata* type.—In these the *Elaiosome* consists of the *raphe*, a portion of the funicle attaching the ovule to the walls of the ovary, and persistently adhering to the side of the ripe seed, and also the caruncle or strophiole, a growth from the point where the funicle is attached to the seed (hilum). It is this which, in larger fruits, forms the aril and frequently covers the seed. In the Primrose (*Primula acaulis*) and *Veronica* of the section *Omphalospora*, where there is no raphe, the funicle plays the part of the *Elaiosome*. This class contains *Viola odorata* and some other species, *Luzula Forsteri* and *L. pilosa*, *Allium triquetrum*, *Chionodoxa Luciliae*, *Gagea lutea*, *Scilla amoena*, *S. sibirica*, *Galanthus nivalis*, *Iris ruthenica*, *Asarum europaeum* and *A. canadense*, *Arenaria muscosa* and *A. trinervia*, *Chelidonium majus*, *Corydalis* sp., *Reseda* sp., *Phyteuma*, *Melampyrum pratense*, *Veronica agrestis*, *V. cymbalaria*, *V. hederaefolia* and *Lathraea squamaria*.

3. *Euphorbia* type.—These have a caruncle formed by the enlarged lips of the micropyle. It is very conspicuous in the Castor-Oil bean (*Ricinus communis*), but can be of little use here as an *Elaiosome*, as the seed is too heavy to be transported by ants. To this group belong *Euphorbia*, *Mercurialis annua* and *M. perennis*, *Buxus*, *Claytonia perfoliata* and *Viola elatior*.

4. *Polygala* type.—In these there are two *Elaiosomes*, one small one at the top, the other larger at the base, *Polygala vulgaris*.

In all these a portion of the seed or its attachment forms the *Elaiosome*. In the rest, in which the fruits are nutlets, portions of the receptacle or pericarp or perianth form the *Elaiosome*.

5. *Hepatica* type.—In this the oil-body (*Elaiosome*) is formed of a portion of the pericarp, which remains attached to the base of the nut or seed. Such plants as possess this system are :—*Thelygonum cynocrambe* (*Cynocrambaceae*), *Adonis vernalis*, *Ranunculus ficaria*, *Hepatica triloba* (*Ranunculaceae*), *Fumaria capreolata*, *F. officinalis*, *F. spicata*, *Platycapnos* sp. (*Fumariaceae*), *Potentilla alba*, and *Waldsteinia geoides* (*Rosaceae*).

6. *Parietaria* type.—These have a small swelling at the base of the nut, formed of the base of the perianth and receptacle, *Parietaria lusitanica* and *Polygonum capitatum*.

7. *Ajuga* type.—In these the oil-body is formed of the part of the receptacle which is attached to the nutlets. These are all species of the orders *Labiatae* and *Boraginaceae* and include *Anchusa arvensis*, *A. sempervirens*, *A. officinalis*, *A. italica*, *Borago officinalis*, *B. laxiflora*, *Myosotis sparsiflora*, *Nonnea ventricosa*, *Pulmonaria officinalis* and *P. mollissima*, *Symphytum officinale*, *S. bulbosum* and *S. orientale* (the *Elaiosome* of this species is large and white, cylindrical, thick, and contrasts strongly with the black nutlet), *Ajuga orientalis*, *A. pyramidalis*, *A. reptans*, *Lamium album*, *L. maculatum* (these plants and *L. purpureum* are constantly to be found on walls at some height from the ground, and probably carried here by ants), *Rosmarinus officinalis*.

8. *Aremonia* type.—This has a cylindric fleshy body, apparently formed from the flower-axis of the nut, *Aremonia agrimonioides* and *Thesium alpinum*.

9. *Carex* type.—In some species of *Carex* the base of the utricle forms an oil-body, e.g. *Carex digitata*, *C. montana*, *C. ornithopoda* and *C. verna*.

10. *Compositae* type.—In some of the *Compositae* there is an oil-body formed by a claw at the base of the achene, e.g., *Galactites* sp. and *Carduus pycnocephalus*. These fruits also possess a plumed pappus, and are widely dispersed by wind. *Trichera arvensis* and *T. atrorubens* and *T. orientalis* have a circular undulate oil-body surrounding the fruit at the base. They are also plumed fruits. *Amberboa* has only a short spiny pappus and an oil-body of a similar nature to that of the last-mentioned plants at the base, or in *A. Lippii* and *A. maroccana* on the side of the fruit, or even terminal as in *A. leucantha*. *Centaurea* has a much reduced pappus and basal oil-bodies, *C. cyanus*, *C. depressa*, and *C. ochroleuca*, as well as *Scabiosa montana*, *S. axillaris* and *S. dealbata* (*Dipsaceae*).

11. Grasses.—*Melica nutans* and *M. major* have an oil-body formed at the base of the spikelet, and *Triodia decumbens* has two similar bodies. The first two are, however, mainly wind-dispersed, and *Triodia* by adhesion.

Ulbrich (in his work on " Dissemination of Seeds ") points out that the presence or absence of an *Elaiosome* is correlated with the other adaptations for dispersal of the seed. In the Primrose (*Primula acaulis*), where the solitary capsules on a slender pendent stem hang towards the ground and drop the seeds in a pile together, the *Elaiosome* is present, while in the Oxlip (*P. elatior*), where the capsules are borne on an erect peduncle, and the seeds dispersed by the shaking of the wind scattering them in different directions, the seeds do not possess an *Elaiosome*. Further, the ant-dispersed seeds of the Primrose are ripe early in the year when ants are at work, while those of the Oxlip are not ripe till October, by which time the ants are retiring into winter quarters. In the Wood Anemone (*A. nemorosa*), the inflorescence is nodding, and the fruits are ripe in April or May. They have a thick pedicel which serves as an *Elaiosome*, while in *A. sylvestris* the stem is erect, stiff, woody, elongate, and the fruit ripens in July and August. It is dispersed by wind-action, and the achenes have no *Elaiosome*.

The number of seeds carried off by ants, and the distances to which they are borne, have been noted by several observers. Sernander observed *Aphenogaster* carrying 216 seeds in 3 hours, and *Formica rufa* carried off 366 seeds in 19 hours, of which there were 156 seeds of *Melica*, 69 of *Melampyrum*, 21 of *Luzula pilosa*, 28 *Hepatica triloba*, and 25 *Carex digitata*. Assuming that these ants were at work on 80 favourable days in the year for 12 hours a day, the number of seeds transported would be 36,480. Many of these would, no doubt, be buried in the nest, but he found that there were many left outside with the oil-body bitten off, and many were dropped on the way. To find out the number dropped *en route*, he staked out a square metre on a path through a wood, largely used by ants, where *Melampyrum* was abundant, and counted 28 seeds left by them on the path. We have other evidence as to the rapidity

and quantity of the seeds carried off by them in Lock's observations on *Turnera*, described below, where *Pheidole* carried them off at the rate of more than one a minute and 200 in 2 hours.

The distance to which seeds are carried are given by Sernander as from 15 to 70 metres (45 to 210 feet).

Most of the observations which have been made have been derived from the study of European ants, but this form of dissemination is found all over the world, and is important in the tropics, where ants are vastly more abundant than in temperate regions. It seems clear that they perform important functions in the dissemination of epiphytes, apart from their action in supplying soil to these plants, as I have shown in my paper on Ants and Plants (*Ann. Bot.* xxiv, 457). I will, however, first give notes on the action of ants in temperate northern regions. Kerner states that *Tetramorium caespitosum* is indefatigably engaged throughout the summer in collecting seeds and dragging them to its nest, and *Lasius niger* and *Formica rufibarbis*, which live in holes in the earth and hollow trees, also collect caruncular seeds and carry them to the nest. He notes that it is seeds with smooth external coats and large caruncles that these ants carry off, such as those of *Asarum Europaeum* and *A. canadense*, *Cyclamen europaeum*, *Galanthus nivalis*, *Arenaria muscosa*, *Sanguinaria canadensis*, *Viola austriaca*, *Vinca herbacea*, *V. minor*, and various *Euphorbias*. *Chelidonium majus*, he says, in the Botanic Gardens of Vienna, is a constant feature of ant-runs, and, indeed, it may often be seen in England in banks, on ruins, and such spots, where ants habitually go. Lundstrom mentions the carrying off of the seeds of *Melampyrum*, the Cow-wheat, when fallen from the plant. Jean Massart (in "La Dissémination des Plantes Alpines") says that near the Staffel Alps, in Switzerland, at 2,200 metres altitude, he found a nest of *Formica rufa* composed of twigs and fruits of *Juniperus communis*.

F. W. Weiss (*New Phytologist*, vii, p. 26, and vii, p. 81) adds to our knowledge of the subject. He observed a curious distribution of the common Gorse (*Ulex europaea*) along roadsides and over disused tracks in moorlands. In some cases the gorse was distributed in a line across an open heathland where there had been, or still was, a cart track, and frequently bushes occurred in close proximity to the nests of the big Wood Ant, *Formica rubra*. On placing 5 seeds of the gorse on the ant's run-way, all were carried off in 10 minutes, and of 9 seeds, all but one, with a shrunken and discoloured caruncle, were carried off in ¼ of an hour. The gorse seeds are provided with a bright orange caruncle containing a large amount of oil. Similar observations were made by him and Mr. Tansley with respect to the Broom (*Sarothammus scoparius*), which possesses a similar caruncle, of which 5 seeds were removed by the ants in 18 minutes. The ants turn the smooth seeds about and, when they find the caruncle, bite and tear at it and finally carry the seed away. It seems that frequently they drop the seeds on the way after eating off the caruncle, but sometimes convey the whole seed to the nest. In investigating the contents of the ants' nest, he found 27 fruits of *Anthoxanthum odoratum* (the Sweet Vernal Grass) found also by Sernander in the nest of *Lasius niger*, who saw ants carrying them along, but which were more likely blown to the nest by the wind, *Hypochaeris radicata*, *Arrhenatherum avenaceum* and *Rumex crispus*, doubtless brought by the wind, together with seeds of *Senebiera didyma*, *Cotyledon umbilicus*, *Stellaria holostea*, *Luzula campestris*, *Conopodium denudatum*, and the Gorse, only the last-mentioned is known to be sought for by the ants.

These ants, however, frequently carry small bits of wood (and Weiss specially mentions dry winter buds of the oak) and all kinds of small pieces of vegetable matter, to help build up the great mass of debris which forms their nests, and they may carry seeds as well.

The Gorse and Broom both possess explosive capsules, which, on their

sudden dehiscence, throw the seeds to some little distance, but hardly far enough to be very effective as dispersal agents. In fact, they only throw them a few feet from the bushes. This may be compared with the explosive capsule of the violet, which also possesses a caruncle, and is sought and carried off by ants. Some very interesting accounts of the transportation of seeds of herbaceous plants are given by J. T. Moggridge (in "Harvesting Ants and Trap-Door Spiders," 1873). The studies were made in the South of France, chiefly on the Ant *Atta barbara*. These ants carry off not only the seeds, but bite off ripe capsules of such plants as *Capsella Bursa-pastoris*, *Stellaria media*, and the calyces of *Calamintha* containing nutlets. "Where you see little patches "of *Fumaria*, *Avena*, *Urtica membranacea*, *Veronica* (4 species), *Spergularia* "*rubra*, *Chenopodium*, *Rumex bucephalophorus*, *Calendula arvensis*, *Antirrhinum* "*orontium*, *Linaria simplex* and *Cardamine hirsuta*, you may safely expect "to find a colony of *Atta barbara*. The presence of seedlings of these and "such plants foreign to the wild ground is quite a feature near the nest. "These ants store the seeds in their granaries underground, to feed on them, "and naturally destroy a very large amount of the seeds, but may also drop "them near the nest in carrying them, and it is these dropped and abandoned "seeds which continue to grow."

He examined the granaries, and records finding in them the following seed collected by the ants, or being carried to the nests by them: *Arabis thaliana*, *Alyssum maritimum*, *Silene pseudoatocion* and other species, *Fumaria capreolata*, *F. viscida*, *F. spachii*, *Erodium*, *Lavatera cretica*, *Linum gallicum*, *Oxalis corniculata*, *Medicago*, *Ervum*, *Cytisus spinosus*, *Valerianella cruciata*, *Centaurea aspera*, *Odontites lutea*, *Calamintha nepeta*, *Veronica* (4 species indigenous) and *V.* (*Hebe*) *Andersonii* of New Zealand, *Cynoglossum pictum*, *Polygonum aviculare* and *P. convolvulus*, *Parietaria*, *Amaranthus blitum* in large quantities in the nest, *A. patulus*, *Euphorbia* sp., *Paris quadrifolia*, *Smilax aspera*, *Setaria verticillata*, *S. italica*, *Andropogon ischaemum*, *Tragus racemosus*, and fruits of the Cypress and Plane tree. He quotes Dr. Bornet as having seen the seeds of *Acacia retinoides* piled up near a nest.

Mr. Dymes has given me an account of the seeds found in the nest of *Atta barbara* at Bordighera, which may be compared with the account given by Moggridge above. He sowed the seeds, collected from the nest of this harvesting ant, in sterilised soil, and most of those so obtained germinated. These seeds were as follows:—

Glaucium luteum.—One seed germinated.

Alyssum maritimum.—Silicules mature, immature and dehisced, with hundreds of seeds, many of which were mutilated. Seedlings were produced in great profusion.

Crucifer.—Seed unknown, possibly *Brassica* or *Eruca*.

Helianthemum sp., apparently *H. arabicum*.—These last two seeds did not germinate.

Tunica saxifraga.—Seeds germinated.

Geranium rotundifolium.—Seeds germinated and eventually flowered and fruited freely.

Lotus ornithopodioides.—Only a very few seeds germinated.

Trifolium arvense and *T.* sp. did not germinate. *T. rubrum*.—Seeds germinated.

Foeniculum officinale.—A few seeds germinated.

Mesembryanthemum edule.—Seeds found in large quantity, germinated.

Inula viscosa.—Achenes, without pappus, germinated.

Leontodon autumnalis, *Thrincia tuberosa*.—Achenes without pappus. Some seedlings, but to date too young to identify.

Calendula stellata.—Two fruits found.
Echium pustulatum.—A few nucules germinated.
Plantago Psyllium.—One seed found; germinated.
Chenopodium Bonus-Henricus.—One seed found.
Polygonum aviculare.—A few seeds germinated.
Euphorbia peplus.—Two seeds found. *E. segetalis*, a few seeds with *elaiosome* gone.
Parietaria diffusa.—Very many seeds which germinated freely.
Piptatherum multiflorum.—Very many seeds which germinated freely.

The remainder of the seeds and debris of the nest were sown, and among the many seedlings produced there were no additional species found. The majority of them consisted of *Tunica saxifraga*, *Alyssum maritimum*, *Parietaria diffusa* and *Piptatherum multiflorum*.

Moggridge's list contains the names of many species similar to those of Dymes's list, and both lists together give a good idea of the very large number of seeds of herbaceous plants disseminated by the Harvesting Ants of the Mediterranean region. It is probable that the number would be increased largely by further research.

Helleborus foetidus Linn.—In a paper by T. A. Dymes (*Journ. Linn. Soc.*, xliii, p. 433) the author points out that the seeds do not fall from the capsule singly, as they do in *H. viridis*, but in a mass, attached to a white band of raphial tissue, which is oily and very attractive to snails and ants. This linear mass has the general appearance of some kind of larva, and Ludwig suggests that the resemblance to one induces ants to carry it off, as it were, by mistake. Sernander and Dymes disagree with him on this point, and no doubt correctly. The idea that carunculate seeds resemble insects, and deceive ants and birds into thinking that they are insects, is an old one, for which I do not think there is any justification at all. Such suggestions occur in Lubbock's "Fruits, Flowers, and Leaves." There is no evidence of ants or birds being deceived in this way, and it is exceedingly improbable. A bird that, by some chance, makes an error of such a nature, discovers its mistake immediately, and ants investigate things very carefully before carrying them off, and what may resemble insects to our eyes do not necessarily resemble insects to theirs.

The ants, it appears, usually carry the whole or a portion of the mass into their nests, a position in which the seeds cannot successfully grow, but if these seeds can remain long enough underground unhurt, as is the case with *Ulex* and other seeds, they may very likely eventually be either thrown up by tillage or by worms in their casts.

Mr. Dymes points out that in the case of Sweet Violet (*Viola odorata*) the seeds are actually benefited by the removal or laceration of the caruncle, for such seeds germinate earlier and produce more vigorous plants, especially in the root system, and he gives a figure to show this.

The seeds of *Cytinus hypocistis* (*Cytinaceae*) are believed to be transported from place to place by ants, by Bargagli (*Bull. Soc. Bot. Ital.*, 1899, p. 203). This plant is parasitic, and it is difficult to see how seeds of a plant of this nature could get to a fresh host without such method of dissemination. In *Buxus sempervirens*, the Box tree, the seeds dispersed primarily from an explosive capsule, are provided with a caruncle, as in other *Euphorbiaceae*, and are probably further disseminated by ants. Sir John Twisden writes me that in his garden at Brabourne, Kent, he finds young seedling Boxes 30 feet from the nearest tree, which he knows fruits, but only 11 feet from the nearest bough of another bush which may have seeded. There were, however, 2 large Yew trees between the latter bush of Box and the seedlings, so that it would be impossible for the seeds to have reached the spot where the seedlings grow

by the mere explosion of the capsules. In this case I have little doubt that the seeds were transported by ants, which are abundant in the garden.

Scopolia carinthaica (*Solanaceae*) K. Ruppert (in " Dissemination de Scopolia carinthaica par les fourmis," *Act. Soc. Bot. Poloniae*, 1893, p. 201) says that the thin epidermis of the cells of the seeds contain a mixture of fat and sugar which is attractive to ants who carry off the seeds.

Ants in Africa.—Bews (" Plant Succession in the Thorn Veldt ") considers that ants play an important part in spreading seeds of herbaceous and low shrubby plants on the African plains, chiefly by carrying about the seeds of grasses. He found *Tetramorium squamiferum* carrying to its nest seeds of :—*Paspalum scrobiculatum*, *Phalaris arundinacea*, *Hibiscus trionum*, *Teucrium riparium*, *Abutilon sonneratianum*, *Argemone mexicana*, *Sida rhombifolia*, *Nicandra physaloides*, *Indigofera* sp., *Datura stramonium*, *Sonchus* sp., and even such heavy seeds as those of *Cassia occidentalis*. In the seeds of most of these plants there is no caruncle or *Elaiosome*, and they must be carried off to be devoured ; but he notes that those of *Hibiscus trionum* have tufts of glandular hairs, and the nutlets of *Teucrium riparium* are covered with glandular hairs, which may be the cause of attraction to the ants.

Marloth, in his work on the Flora of South Africa, mentions that *Endonema retzioides* (*Penaeaceae*) is disseminated by ants. The seeds are shaken out of the capsules by the wind, and are picked up by the ants for the sake of the large fleshy *Elaiosome* they possess. He also states that the large seeds of *Sterculia Alexandri* are ant-dispersed, the ants being attracted to the seeds by the *Elaiosome*, after the seeds have fallen to the ground, and suggests that the restricted occurrence of the tree, a single patch in the Transvaal, is due to this limited form of dispersal. I have not seen ripe seeds of this plant, which are said to be 2 cm. (1 inch) long. No species of *Sterculia*, so far as I know, has a caruncle. Most of the species are dispersed by birds, and the seeds of this plant seem to me to be too large to be carried off by ants.

Mystropetalon (*Balanophoraceae*), of which there are two species in South Africa, is parasitic on the roots of *Protea*. Marloth states that the fruits, which are very small, are borne on a round receptacle filled with fat. Ants gather the little fruits on account of the fatty body (*Elaiosome*), which they eat, and disperse them in their nests in various directions, buried at a sufficient depth in the soil to enable the haustorium of the germinating seed to reach the root of a *Protea*. He has found seeds of this plant in the nests of ants, deprived of the *Elaiosome*.

Ants in Tropical Asia.—Mr. R. A. Lock (in the *Annals of the Botanic Gardens*, *Peradeniya*, *Ceylon*, Oecological Notes on *Turnera ulmifolia* var. *elegans*) gives an account of the dispersal of the seeds of a species of *Turnera*. The plant he refers to is, however, *T. trionaeflora*, a South American plant, which has been carried about the world as an ornamental plant, and which has become naturalised in many spots as a garden escape. It was thus abundant sporadically near the gardens in Singapore. (*T. ulmifolia*, with yellow flowers, grows only in sandy places, usually near the sea, and has occurred, perhaps as a garden escape, in Christmas Island, Cocos, Bermudas and Seychelles. It appears to be a native of Mexico).

T. trionaeflora is a herb about 1 foot tall, of creamy-white flowers, with a dark purple eye and capsules containing a large number of small seeds, which are pear-shaped and bear at the small end a large shield-shaped aril, covering half the surface, fleshy and soft, and containing starch and oil. The capsule opens at the top in 3 valves and lets the seed fall out. Various species of ants, including *Pheidole spathifera*, carry off the seeds and eat the aril. Lock saw one carry the seed to the mouth of the nest 5 yards away, and 30 seeds carried off at the rate of one a minute, and 200 carried off in 2 hours. The ants carry them off by the aril, and he saw ripe seeds deprived of the aril carried out of

the nest and thrown away. Another ant which disseminated this plant, but to a less extent, was *Camponotus mitis*.

Col. J. H. Tull Walsh (in "Scientific Memoirs of the Medical Officers of the Army of India," vi, 1891) gives an account of some Harvesting Ants in Calcutta. The ants were *Holcomyrmex scabriceps* and *H. criniceps*. These ants first attack the grasses and other plants near the nest, and then go further afield when the supply of seed is scanty or exhausted. He measured a train of ants, over 15 yards long, moving along a well-worn path, and reaching from the nest into a small garden where the worker ants were collecting grain. They climb the stalk, cut off the grain with the glumes, and carry it down or drop it, for the ones on the ground to pick up. These carry off the spikelets and free them of glumes in the nests. He found the granary of a nest of *H. criniceps*, which contained 305 seeds of *Amaranthus gangeticus* grown as a vegetable in the garden, and 22 seeds of *Scirpus* (*Isolepis*) *barbatus*, of which only a few plants could be seen near the nest; this latter is a small sedge about 4 or 5 inches tall, growing in open sandy spots. Besides these two plants, he observed them cutting *Eragrostis plumosa*, *Perotis latifolia*, *Eleusine indica*, *Panicum indicum* and *Cynodon dactylon*. Though they collect seeds from a great variety of plants, they seem to prefer the grains of grasses.

That ants transport small baccate and drupaceous fruits to some distance in the tropics is certain, and in the case of fallen fruits they may disseminate them satisfactorily. I have seen an ant, *Polyrachis*, in Singapore carrying along the succulent berry of the tree *Cyrtophyllum fragrans* to some distance, and then drop it unharmed. Otto Kuntze states that the ants fasten on the fruits of *Carica Papaya* and push them before them in companies of three. In these cases the insects are collecting the seeds evidently for the surrounding sweet and semi-liquid pulp.

It seems highly probable that many of the epiphytic plants with small berries or drupes are transported from one tree to another by ants, such plants as *Myrmecodia* and *Hydnophytum*, for instance. These have small, red, succulent fruits produced singly from a depression in the stems. The Vegetable Ants' nests swarm with vicious biting ants, and it does not seem likely that birds would alight on the plant to collect the rather inconspicuous, shortly projecting fruits. I once put some fruits of *Hydnophytum* in a porcelain dish on my verandah in Singapore, and covered it with a plate of glass, intending to observe the germination. The next morning I found a number of large black ants (not any of the common house-ants, but a much bigger kind) that had somehow invaded the house and were in the covered pan, apparently attempting to attack and carry off the fruits.

Dischidia Gaudichaudii.—Dr. and Mrs. Van Leeuwen (in *Ann. Bot. Buitenzorg.*) give some account of the dispersal of seeds of this little creeping epiphyte (under the name *Dischidia nummularia* (*Asclepiadaceae*)) by the small ants of the genus *Iridomyrmex*. They point out that the plumed seeds of this plant (which is extremely common on trees in open country in the Malay region) drift from the pod when it dehisces in the wind, and, if they come in contact with a bough, often adhere to it. If they do not strike one at first, they drift on further. If they are merely stuck on the bough, they germinate, but soon perish. They observed, however, that the plants grew successfully from the channels on the boughs made by the ant. These ants build nests between the branches and roots of *Dischidia Rafflesiana* and such spots, and form their nests from the enlargements of their tunnels or covered ways, and it is from these that the seedlings of the *Dischidia* grow. When a seed adheres to a bough, the ants run up in great numbers and pull it by the plume hairs. There are two kinds of hairs on the end of the seed, one set long and the other short. The ants pull off the long hairs, and then drag the seed by the short ones to disappear

beneath the leaves and roots of the larger *Dischidia Rafflesiana*, where they germinate and grow.

Though *D. Gaudichaudii* does grow as thus described, about the stems and roots of *D. Rafflesiana*, it frequently grows also on boughs of trees where that species is absent, for it is a plant very much more common. In these cases I suppose the *Iridomyrmex* carries the seeds to nests under the roots of other epiphytes or beneath the loose bark under which it often builds its nests. The tunnels and nests are built of debris of bark, soil, etc., and this probably forms the nutrient soil for the seedling.

Ants in North America.—G. Lincecum, in describing the habits of the Agricultural Ant of Texas (*Myrmica molefaciens*), states that they make pavements of a hard crust of coarse sand and grit, on which no herb except *Aristida stricta* is allowed to grow. The grain of this is harvested, the glumes removed, and then it is stored in dry cells, and he affirms that they even sow the grain. They store up also grains of other grasses, and many herbaceous plants. (A. S. Packard, " Guide to the Study of Insects," p. 185).

Ants in South America.—Ulbrich (" Biologie der Frucht und Samen," 1928) quotes, from Ule and others, instances to show how ants in South America transport the seeds of epiphytes to their mud nests in the trees. Ule states that these ant-gardens in Brazil vary in size. *Camponotus femoratus* builds them as big as a pumpkin, and on these nests he found *Philodendron myrmecophilum* and *Anthurium scolopendrinum* var. *Porteanum* (*Aroids*), *Streptocalyx angustifolius* and *Aechmea spicata* (*Bromeliaceae*), *Peperomia nematostachys* (*Piperaceae*), *Codonanthe Uleana* (*Gesneraceae*) and *Phyllocactus phyllanthus*, while on the smaller gardens made by the species of *Azteca* (*A. Traillii*, *A. Ulei* and *A. olitrix*) he found *Philodendron myrmecophilum*, *Nidularium myrmecophilum*, (*Bromeliaceae*), *Ficus paraense*, *Marckea formicarum* and *Ectozoma Ulei* (*Solanaceae*) and *Codonanthe formicarum*. Wheeler in British Guiana found nests, from the size of a walnut to that of a football, of similar ants with *Camponotus femoratus*, *Crematogaster lineata*, *Anisochetus emarginatus*, and species of *Azteca* on whose mud nests were *Codonanthe* (2 species), *Anthurium* and *Peperomia*, and *Streptocalyx*. The seeds of all these epiphytic plants must have been brought to the nests by the ants and germinated in the mud.

Some Minor Methods of Insect Dispersal.

Transport of Seeds by Caddis Worms.—V. Kindermann (in " Verbreitungs biologische Beobachtungen bei Pflanzen," *Lotos Nat. Zeitschr.*, lix, 7, p. 220) suggests that Caddis Worms (*Phryganidae*) may carry about, attached to their cases, seeds of aquatic or riverside plants such as *Cicuta virosa*, *Myosotis palustris*, *Lycopus*, *Alnus*, *Alisma*, *Sagittaria*, *Iris*, and *Carex*. This is more curious than important in the matter of dispersal. It is quite probable that they would do so, as one often finds snails, small stones, etc., attached to their tubes; but nearly all the plants he mentions have floating seeds which would be more aptly dispersed by water-flow. Still, they might pick up sunken seeds and attach them, e.g., *Myosotis*, and the cases might float away after the escape of the adult insect, carrying the seeds with them. It, however, can hardly be taken into account as an important method of dispersal.

Seeds and Fruits Dispersed by Grasshoppers.—Massart (in " Diss mination des Plantes Alpines ") suggests that a number of small herbaceous plants may have their seeds dispersed by grasshoppers, especially of the genus *Stenobothrus*, which, skipping about among the herbage, may dislodge the seeds from the capsules or knock off small fruits. This, again, has comparatively little importance from a dispersal point of view, but may cause explosive capsules to burst and throw small seeds to a short distance from the plant.

Seeds and Spore Dispersal by Insects by Adhesion.—Guppy (in the "Naturalist in the Pacific," i, p. 509) suggests a possibility of minute seeds, such as those of *Orchids* and *Begonias*, being transported across the seas by insects, which, as he says, can be carried very high into the air, and, borne along by high air currents, might reach places far distant from their home. He mentions the occurrence of large flights of dragon-flies to Cocos-Keeling Island, and the same thing regularly (it appears) occurs on Christmas Island, where they are very abundant, though there is no water for their early aquatic life. Large hawk moths also fly extraordinary distances, such as the Convolvulus Hawk-moth (*Sphinx convolvuli*), which I have caught on Christmas Island, as well as in Kent and Singapore. That these insects might convey seeds as small as those of *Orchids* and *Begonias* is possible, but I have no evidence to offer on the subject.

That insects convey the spores of the lower *Cryptogams* from place to place is undoubted. At the same time it is to be noted that, as shown in the section dealing with wind transport (p. 50, etc.), the spores are so light that in very many cases they can be, and are, conveyed long distances by wind alone. The spores of fungi and algae, as well as bacteria, are the chief classes to be thus transported.

Moss Spores Dispersed by Flies.—In the *Bryologist*, 1912, p. 1, J. Bequaert gives a curious account of the dispersal of the spores of a species of *Tetraplodon* (*T. minioides*), and (in the *Biol. Centralblatt.*, 1897, p. 48) N. Bryhn gives a somewhat similar account of a species of *Splachnum*. All the mosses of this section grow on dead animals or dung, and it seems clear that the flies, attracted by the mosses transport the spores to other suitable habitats for them. Bequaert observed in the Adirondacks that some small flies belonging to the genus *Phorbia* licked the top of the hypophyses of the moss, and in doing so they came in contact with the spores at the mouth of the capsule. The hypophyses appear to be conspicuous, both in *Tetraplodon* and *Splachnum*, when the spores are being discharged, and Bequaert noted that the cushions of *Tetraplodon* had a strong fruit-like odour, which might serve to attract the flies. In the case of *Splachnum*, the flies found by Bryhn were not identified. He describes them, some as like house-flies, others like dung-flies. He counted the visits of the flies, which were 50 in ½ an hour. The flies were all covered with the spores of the *Splachnum* (*S. rubrum*) uniformly on the underside, or in a large patch on the thorax. The moss grew on cow's dung, and the flies flew to a fresh patch and walked over it.

The moss is specially adapted for this method of spore-dispersal. It grows, like *Tetraplodon*, in masses or cushions, so that the flies can walk on it. The hypophyses are coloured, especially bright in the *Splachnum* when the spores are ripe, and the spores are not loose and powdery, as in most mosses, but are sticky, and adhere in masses.

Lichens are also probably dispersed to some extent by insects in much the same way as other cellular Cryptogams. Darbishire (in "Deutschen *Pertusaria*," *Engler's Jahrbuch*, xxii, 293) noted frequently that small *Poduridae* (*Collembola*), in moving over the surface of the Lichen *Pertusaria amara*, became powdered over with the soredia, and evidently took considerable part in the dissemination of the species.

Fungi.—In the matter of dispersal of spores of the Fungi, insects play a somewhat important part. Mr. Butler, in a paper on the dissemination of parasitic fungi, writes: "The ergots of Rye (*Claviceps purpurea*) are carried "about in part by flies such as *Melanostoma mellina*, *Rhagonycha fulva*, etc., "which are attracted by the sugary excretion that accompanies the sphacelia "stage of the fungi, and carry the spores to other grasses. Pearblight (*Bacillus* "*amylivorus*) begins often in the stigma to which the bacillus is carried, chiefly "by bees, from the infected sap escaping from the bark in spring. In *Sclerotinia*

"*urnula* the sweet-smelling spores are carried by insects to the flowers of "*Vaccinium vitis-idea.*"

I have seen flies (*Musca*) visiting *Cerebella paspali*, parasitic on grasses, in Malaya, constantly sucking at it on the flower spike of *Paspalum longifolium*, and flying on to other grass spikes. *Dictyophora phalloidea*, like *Phallus impudicus*, is a great attraction to flies. The spores are embedded in the brown or green, foul-smelling mucus, and, as Massee says, the flies carry the spores on their legs and proboscides, and he states a copious growth of mycelium has been obtained from their excrements.

The chief dispersers of fungus spores and bacteria are to be found among the Flies (*Diptera*), the *Homoptera* (*Aphis*, Frog Hoppers), and *Hemiptera*, but many other insects may act as transporting agents. The sucking insects, especially those with perforating beaks, are responsible for the transference of spores from one plant or animal to another. The story of these is practically the story of plant disease, and is to be found in all works dealing with the subject, and this method of insect dispersal is so well known that it is unnecessary to dilate further upon it. It is, however, to be noted that most spores of parasitic fungi can be also transported by wind.

Beetles occasionally act as dispersers of bacteria, and probably also of fungus spores. F. V. Rand and L. C. Cash describe the dispersal of bacterial wilt in corn by beetles (in *Science*, N.S., lix, 1516, pp. 66, 67) saying the 12-spotted Cucumber Beetle (*Diabrotica duodecempunctata*), introduced into cages of maize seedlings, infected them with *Aphanobacter Stewarti* to a small extent. The intestinal contents of insects fed on diseased plants were inoculated into 85 plants, of which 15 were found later to be infected. The Flea-Beetles (*Chaetocnema pulicaria* and *C. denticulata*) are responsible for the mid-season spread of the disease.

Insects of small size as well as large ones seem to travel by air to long distances, and, as has been mentioned under Wind Dispersal, small ones have been captured at considerable altitudes in spore traps taken up by aeroplanes. Guppy records their occurrence at very high altitudes in Hawaii. That they cross the sea for long distances is shown by their occurrence very early in oceanic islands, so that there can be no difficulty in their transporting minute spores. At the same time Butler's observations on the slow progress of fungal diseases of plants must be taken into account, as showing that fungi do not always move as fast as one might expect.

Besides their flight and drift on the wind, insects may reach oceanic islands on drift timber or on pumice. Ants arrived quite early on Krakatau, and are to be found on almost all oceanic islands, and could only come to land in some such method, and thus insects might bring spores of fungi with them.

Dispersal by Crustacea.

The land-crabs, which often feed on fallen fruits, may carry them to some little distance. In Christmas Island the Red Crabs (*Gecarcinus*) were very partial to the fruits of *Inocarpus edulis*, of which they ate the green husk. As they drag them from some distance to their burrows for this purpose, it is not uncommon to see a dozen or more young plants growing in a circle round the mouth of the burrow. They are also very fond of the fruits of *Terminalia catappa*, and eat also the fruits of *Sideroxylon sundaicum*. Certainly the *Inocarpus* and *Terminalia* have been diffused over the island by these animals.

Crabs, however, are undoubtedly the cause of the destruction of many sea-borne fruits which are drifted upon the shores of islands or mainland, by biting off the plumule when they germinate. The destruction, too, of Coco-

nuts by *Birgus latro*, the Robber Crab, may account for the absence of the Coconut from many islands and shores, and they destroyed great numbers of the seeds of the endemic Palm *Arenga Listeri* in Christmas Island, crushing the seeds and not eating the pulp.

Snail Dispersal.

In the paper by Mr. Dymes on dispersal of the seeds of *Helleborus foetidus*, he gives an extensive account of dispersal of these seeds by snails, which devour the oil-body (*Elaiosome*), and in so doing get some of the seeds adhering to their bodies. The snail appeared to resent the adherence of seeds to its head and tail, and sloughed them off, but was quite unconcerned if the seed stuck to its body near the shell on the head side, and one carried a seed thus for 14 inches. He also records the snails carrying seed of *Geranium Robertianum* and of Stocks. The snail *Helix asperata* travels 2 inches in 1 minute, or 1 mile in 22 days, and though the pace and distance a snail travels are by no means great (he has observed snails travel 18 feet for food), still, in time they must get over a fair area, and, as these molluscs are very abundant and widely spread over the whole country, there is no reason to doubt that, if they commonly carry seeds in this manner, they would equally soon distribute plants over an equally large area in the same time that it takes them to distribute themselves.

M. W. Beyerinck (in *Gardeners' Chronicle*, 1883, p. 823) gives an account of the dispersal of strawberry achenes by snails. He fed the large garden snails, *Helix pomatia*, on strawberries, and, on examining the excreta, found a considerable number of the minute fruits had passed unharmed. He planted these achenes, and raised several healthy plants from them.

Dispersal of Fungi by Snails and Slugs.—Massee (in "Diseases of Cultivated Plants and Trees," p. 197) writes:—"Snails and slugs are "responsible for the spread of spores. Many kinds of fungi are eaten by "slugs, and, as far as is known, the spores of some fungi only germinate "after passing through a slug. Slugs are eaten by toads, and this is another "agent. They also carry spores in their mucus." P. Voglino ("Richerche intarno al azione delle lumache nello viluppo de Agaricum," *Nuovo Giorn. Bot. Ital.* 27, 1895, p. 18) and Buller (l.c.) say that slugs eat fungi readily, and germinating spores of *Tricholoma humile*, *Mycena alkalina*, *Inocybe fastigiata*, *Lactarius deliciosus*, *Russula*, and *Hebeloma saxatile* have been found in the viscera of slugs. F. Ludwig ("Die Beziehung zwischen Pflanzen und Schnecken," *Centralblatt Bech.*, 1891, p. 35) also gives an account of dispersal of fungus spores on plants by snails.

Dispersal by Earth-Worms.

Beccari (in Malesia iii, 325) has treated of the probable dispersal of seeds by earth-worms. He found the saprophytic Orchid *Epipogum Gmelini* in abundance in Italy in a ground full of earth-worms, and suggests that they might swallow the seeds, and being afterwards swallowed themselves by birds, the seeds might be borne away by thrushes or other birds, enclosed in the intestine of the worm, and later ejected by evacuation at a distant spot. He observed that Thrushes (*Merli*) and Ortolans (*Beccacie*) frequented the spots in which these worms were abundant, and fed on them. He put seeds of *Mimulus cardinalis*, *Gesnera tubiflora*, *Digitalis purpurea*, *Gentiana cruciata* and *Petunia violacea* in a pot of damp earth with worms. In 24 hours the worms evacuated the previously swallowed earth. He dissected a worm and found in its intestine 50 *Digitalis* seeds, 20 *Mimulus* seeds, 11 *Petunia* seeds, 5 *Gesnera*,

2 *Gentiana*. He fed the worms with Crucifer seeds, which proved fatal to them. However, he found 1 seed of *Cochlearia officinalis* in a worm. Examining the excreta of some other worms, he found some seeds therein—*Trifolium* 1, *Draba verna* 4, *Cerastium* 1, *Compositae* 1, Grass 1, *Veronica* 1, *Labiata* 1. He suggests that the seeds of the minute jungle plants *Thismia*, *Burmannia*, *Gymnosiphon* (*Burmanniaceae*), *Epirhizanthe* (*Polygalaceae*), and *Cotylanthera tenuis* (*Gentianaceae*), and some of the small Orchids, and perhaps *Cyrtandra* (*Cyrtandraceae*) might be distributed in the same way by worms. The little saprophytes certainly have a curiously wide distribution, but are apparently absent from oceanic islands. If they are dispersed as Beccari suggests, the most likely birds to effect this in Africa, Malaya and Australasia, are the Ant-Thrushes (*Pitta*), which are migrant birds, and haunt the densest parts of the jungle where these saprophytes grow, feeding on worms.

Another way in which earth-worms may assist to some extent in moving seeds and planting them, is by drawing them into their holes. Darwin (in "Vegetable Mould and Earth-Worms") quotes Hensen (*Zeitschrift für Wissenschaft Zoolog.*, B, xxviii, 1877, 366) as saying that he found as many as 15 seeds of pear having been carried down into a single burrow, one of which had germinated, and that Mr. Lindsay Carnegie found the chambers of the worms containing the husks of flax seeds, and "they must also contain living "seeds, for on the following spring Mr. Carnegie saw grass plants sprouting "out of some of the intersected chambers." I have seen them pulling the valves of the pods of *Robinia pseudacacia*, with seed attached, into their holes, and Mr. Dymes tells me that the fruit of *Arum italicum* is drawn into their burrows by them. It is probable also that earth-worms disperse the spores of subterranean fungi to a considerable extent, and W. Gleiberg (in "Nachtrich en Blatt. Deutsch. Pflanzenschutz dienst," ii, 11, p. 89) gives an account of the dispersal of the Clubroot of Cabbages (*Plasmidiophora brassicae*) by these animals, showing that, when feeding on or penetrating decaying cabbage, they disseminate the disease in their excreta.

CHAPTER VI

DISPERSAL BY SIMPLE ADHESION

Dispersal by Adhesion of Seeds or Fruits to Animals, the feet of Man, Carts, etc.—Portions of Living Aquatics transported by Birds, Batrachians, etc.—Seeds and Small Fruits transported on the feet of Birds—Isolated Ponds and Distant Marshes—Small-seeded Plants in Islands.

DISPERSAL BY ADHESION OF SEEDS OR FRUITS TO ANIMALS, THE FEET OF MAN, CARTS, ETC.

A LARGE number of plants owe their distribution over wide areas of land to the adherence of their seeds or fruits, or even portions of the vegetative organs, to fur, feathers, or feet of passing birds and mammals. Seeds or small fruits may be merely attached to the feet of a bird or other animal by the mud through which it walks, or on which it sits, without possessing any specialised apparatus for attachment, or they may be furnished with hairs, or hooks on seed, fruit, calyx or bracts, by which they may cling to the animals, or they may possess a viscid, gummy exudation by which they become glued to some portion of the passing traveller with whom they come in contact. Added to these methods of dissemination it sometimes occurs that plants are dispersed by fragments of the branches or stem, with or without fruit attached, which from hooked bristles or viscid excretion, or (especially in water plants) by simply clinging to a bird or mammal, can be borne to a distance. The fragments, continuing to grow after being detached from their carrier and dropped in some suitable spot, thus act in dispersing the species, or, if in fruit, the seeds being detached *en route*. Usually, when the carrier comes to rest, it disembarrasses itself of the attached seeds, fruit, or branch, and leaves them on the ground. Occasionally the incumbrance is brushed off by the vegetation it passes through, or, in such cases as the wool of sheep, the locks containing the seed or fruit are shed from time to time, so dispersing it.

It is not, however, that wild mammals and birds are the only dispersers of adhesive plants. Many, especially of the small and herbaceous plants, are now very widely disseminated by the adhesion of seeds or fruits to the feet or clothing of man, or to the fur or feet of his domestic animals, to the wheels of carts, etc.

Most of the plants disseminated by adhesion in these ways are small herbs or low bushes, not above 3 or 4 feet tall, as if the fruits were borne higher on the plants, they would be too tall to come into contact with the passing animal destined to transport the seeds ; but there are some fairly big trees which possess viscid fruits which are destined for transport by birds which settle in the branches. Such is the remarkable genus *Pisonia*.

In the matter of minute spores of cellular Cryptogams, it is mentioned here that, owing to their small size and frequent exudation of mucus which they produce, they are readily attached to fur or feathers, as also to the bodies of molluscs, earthworms, and insects. Massee says that birds, rabbits and hares carry

spores of fungi about, and Yeates states that *Lunularia*, a hepatic, is dispersed by the attachment of its spores to rats. The story of the dispersal of spores by insects and molluscs, etc., is given under the head of dispersal by these animals.

Though it is highly probable that most of the seeds of the herbs common on roadsides and ploughed fields owe much of their distribution to their becoming attached in mud to the feet of men and domestic cattle, the amount of actual proof of this is not great.

Mr. Woodruffe-Peacock (in " A Fox Covert Study ") gives a list of plants he has observed in mud attached to boots. They are the following :—*Carex sylvatica*, *Poa trivialis* var. *nemorosa*, *Juncus conglomeratus*, *Scilla nutans* (*Hyacinth*), *Rumex nemorosa*, *Stachys sylvatica*, *Taraxacum dens-leonis*, *Lactuca virosa*, *Picris echioides*, *Mentha verticillata*, *Veronica agrestis*, *Ajuga reptans*, *Lychnis alba*, *Vicia cracca*, *Conium maculatum*, *Ranunculus auricomus* var. *depressus*.

Miss Brenchley (in " Weeds of Farm-Land ") records finding by a gate between a public road and a ploughed field the following plants, the seeds of which were brought by the feet of human beings, or of cattle, or on cart wheels :—*Alopecurus agrestis* (slender Fox-tail Grass), *Lolium perenne* (Rye Grass), *Triticum repens* (Couch Grass), *Phleum pratense* (Cat's Tail), *Euphorbia exigua* (dwarf Spurge), *Chenopodium album*, *Rumex obtusifolius* (broad-leaved Dock), *Veronica agrestis* (Field Speedwell), *Anagallis arvensis*, *Plantago major* (Great Plantain), *Carduus arvensis* (Creeping Thistle), *Potentilla anserina* (Silver Weed), *Brassica arvensis* (Charlock); and on mud carried by cart-wheels :—*Capsella Bursa-Pastoris*, *Senebiera coronopus*, *Anthemis arvensis* (Chamomile), *Anthemis cotula* (Mayweed), *Spergularia arvensis*, *Papaver* sp. As she usually only gives in these lists the English names of these plants, I have added the scientific names, which I suppose are those of the plants she intended.

Mr. Worsdell (in *Gardeners' Chronicle*, 1903, p. 101) states that the seeds of *Colchicum autumnale* (Meadow Saffron) are viscid and become attached to the feet of cattle, which thus convey them from one field to another. Most of these plants have other methods of dispersal. Thus the Thistle, Dandelion, etc., have plumed seed, and are certainly more commonly diffused by the wind. *Potentilla anserina* is eaten by geese, and river-dispersed, and so carried about. Many of the grasses are eaten by animals, and the seeds so diffused, and other plants (Hyacinth, etc.) are mainly dispersed by rain-wash and ants, but the action of man and his domestic animals increases the spread of these weeds largely over cultivated ground.

Praeger (l.c.) examined the mud scraped from the boots of a Clare Island man on his arrival at the island, and found it to contain the seeds of the following plants :—*Stellaria media*, *Conium maculatum*, *Sonchus asper*, *Anagallis arvensis*, *Polygonum aviculare*, *Juncus bufonius* and *Juncus* sp., and *Holcus lanatus*. He also mentions finding achenes of *Matricaria discoidea* in mud on his own feet. T. H. Willing (*Journ. Dept. Agric. New Zealand*, I, 66, 1910), says of *Thlaspi arvense* : " The seeds are very easily carried on thrashing machines or other " implements, and are easily carried about in the mud on a boot, or on the feet " of horses or other animals, as well as on the wheels of carts."

The occurrence of *Stellaria media*, the Chickweed, in the Macquarie Islands (and many other spots) may be due to the adhesion of its seeds in mud to the feet of sealers visiting the island. *Plantago major*, now widely distributed in cultivated ground all over the temperate and subtropical regions, is so closely associated with man that it is said to be called " White Man's Foot " by the North American Indians. *Vicia cracca*, which is recorded above by Woodruffe-Peacock as found attached to the mud on boots, is said to mark the former abodes of Norwegian colonies in Greenland.

In Redlands Woods, near Dorking, Surrey, I found one year that in the

cart tracks through the woods made by the timber-cutters' wagons, the ruts were full of water, and contained abundance of plants of *Callitriche verna*, evidently brought on the feet of the horses or on the cart wheels, either as seed or portions of the plant from the open country or the common, some considerable distance away. There was no place for it in the woods themselves.

M. S. Bebb (*Bot. Gaz.*, vii, 69), dealing with the introduction of plants into Rockford, Illinois, in North America, mentions that *Lactuca scariola* was introduced into the country and spread along rainways. A patch of it near the railroad at Rockford was disseminated along the roads by adhesion to cart-wheels.

Even in the rice-fields many of the weeds are introduced on the feet of buffaloes and other animals, as well as by wading birds. E. Quisembing (*Philippine Agric. Journ.*, xiii, 210) states that the sporocarps of *Marsilea crenata* (*Marsileaceae*) are disseminated on the feet of water-buffaloes (used in ploughing the rice-fields) and dogs, as well as by the birds which wade about the rice-fields in search of fish, crustacean, and other animal food. (For the dispersal of seeds by waders, *see* " Isolated Ponds," p. 546.)

Matricaria discoidea D.C. (*M. suaveolens* Buch.) is a small inconspicuous annual, about 4 to 6 inches tall, and has smooth light achenes 1 mm. long, quite unprovided with any particular means of dispersal. They do not appear to be even viscid when wetted, and I have failed to make them attach themselves to my clothes. When ripe, they become detached from the receptacle, and are partially covered by the involucral bracts, which, when they are dry, curve over them in the same way as one sees in the common Daisy (*Bellis perennis*). Holding the achenes in my hand about 2 feet from the ground, I found that in a strong wind they were blown 3 or 4 yards only before falling to the ground. At the normal height of the plant they would not, of course, go so far. They might, however, if the ground was open, be blown along for some distance, and they appear also to be carried along by rain-wash. The plant in England is strictly a roadside or pathside plant. I have not seen it anywhere where people do not habitually walk. It grows on the edges of roads, not in the centre, nor away from the edge. Near Puttenham, in Surrey, I found it on the edges of a track from the main road (where I did not see it) to a cottage, the path being only used by cottagers. In a piece of waste ground at Kew it appeared when the ground had been cleared and rubbish piled about on it, in the centre only, where people used to walk, from the direction of another patch of it at some distance away on the road. I could not find it anywhere else in the neighbourhood. After a heavy fall of rain I walked through a fruiting patch of it on a road at Kew, and after returning home, about ½ a mile walk, I found at least a dozen fruits attached to my left boot between the upper leather and the sole, and several more on the right foot (September, 1926). In Perthshire I found a cattle yard crowded with plants of this *Matricaria*. In this case I had no doubt that the cattle had brought them in on their feet. And near Bude, in Cornwall, it was abundant at spots where sheep used to go for shade and water, and it is certain that they carried the fruits on their muddy feet, and perhaps, by lying down on it, in their wool. On Holmwood Common, Surrey, I have seen plants lining the sides of runnels leading from a path where it was plentiful, and the achenes had clearly been carried by rain-wash into the runnels from the path. The achenes on the main path had doubtless been carried on the feet of human beings, as cattle and horses did not go on these paths. Praeger (in a " Survey of Clare Island, in Ireland") writes of this plant :—" In a very small amount of mud scraped off my boots, " on arrival at the island from Achil Sound, in October, I found 4 seeds of "this species." In Guernsey I found it growing along the edges of a triangular piece of grass formed by the meeting of three roads, and I could not find another plant anywhere else for many miles. This plant has been found

apparently wild in Kamschatka, but it was first discovered by Douglas in California in 1833. It later spread all over North America, and later still all over Europe. It appeared in Berlin about 1853, Konigsberg in 1862, and Dorpat in 1869. The same year it was first found by Thomson at Kew, and since then has spread all over the island from Cornwall to the Orkneys, the Channel Islands and Ireland. It reached Palestine in 1877, and New Zealand in 1873. It probably arrived in Europe originally in pot-plants, seed, or soil, in botanic gardens, and, having accidentally escaped, was carried on the feet of man and animals all over the area in 50 years.

This illustrates the rapidity with which an introduced plant can travel when it finds soil congenial to it.

A. H. Hansen (*U.S.A. Dept. Agric. Circular* 165) gives an account of the dispersal of the small creeping Lawn Pennywort (*Hydrocotyle rotundifolia*) in North America. This Umbellifer is a small plant with a creeping rhizome, very slender, with small, round, lobed leaves about ¼ inch across. The very small fruits are borne in a cluster on a short stalk 1/5 inch long. The plant was first cultivated in America from 1890 to 1895, as an ornamental plant for borders and flat-bedding, and in rockeries. It is a native of India and the Malay region, but is now a nuisance in Pennsylvania and Kentucky, infesting lawns and golf links and greenhouse beds, and quite covering them with a dense mat of foliage, to the exclusion of the grass. He attributes its dispersal on golf links and lawns to the mud on the shoes of golfers and others walking over the grass in wet, muddy weather. As in most plants of this type with long, branching rhizomes, its creeping habit gives it a great advantage over low herbage, which it effectually covers eventually, and not only shades out with its leaves, but prevents seeds of other plants settling on the ground. However, I have not seen or heard of this Pennywort behaving like this in the East Indies. In Singapore it grew on a few gravel paths in the Botanic Gardens in small patches, and in the flora of Ceylon Dr. Trimen found it only as a mountain plant, and fairly common at some altitudes.

The distribution of seeds or small fruits by their attachment to the feet of wild animals I have little evidence of. It was probably very extensive in Europe in Pleistocene days, when this continent abounded in hordes of wild horses, bisons, wild ox, elephants and rhinoceros. The extensive distribution of many of our small-seeded herbs may be due either to their adhesion in mud to the feet of the animals, or to their having swallowed the seeds in feeding on the plants, and it is seldom that we get evidence on the subject from living wild beasts at the present day. It is, perhaps, sufficient to note that this method is one way of accounting for the wide dispersal over continental areas of such plants.

I have, however, one piece of evidence that wild beasts do carry small seeds on their feet in mud for a considerable distance.

In the dense hill-forest of Gunong Tungul, in the Dindings, on the west coast of the Malay Peninsula, I once came across the footprint of a rhinoceros in the deep mud of a track. It was full of water, and this was quite filled up with *Nitella microcarpa* (*Characeae*), which, though apparently not a common plant, has been found in Ceylon, South Africa, and North and South America.

The seed of this plant must have been brought by the rhinoceros in mud on its feet, and, as it stamped in the mud, became dislodged, and the rain having filled the depression, it germinated and grew large enough quite to fill up the water. There was no spot in the forest where it could grow, and it is most probable that the animal had picked it up in the distant rice-fields some miles away, as the rhinoceroses often visited these places to feed. These animals are known to ramble great distances, often making a regular round through

the country for as long as a month, so that they might convey small seeds like this for many miles.

An interesting account of the dispersal of seeds and living fragments of plants in North America by the American bison is given by E. L. Berthoud, under the title of "A Peculiar Case of Plant Dissemination" (*Bot. Gaz.*, xvii, 1892, 321). The bisons, when abundant, used to migrate in vast herds across America from the Missouri to Texas, from time to time making large tracks across the country, and along these tracks and round the buffalo-wallows Berthoud found :—*Plantago* (2 species), *Asclepias syriaca*, *Thlaspi*, *Trifolium*, *Amaranthus*, *Chenopodium album*, *Proboscidea Jussieui*, *Sinapis*, *Portulaca*, *Lippia cuneifolia*, *Cenchrus*, *Stipa*, *Setaria*, *Elymus*, *Dactylis*, *Deschampsia*, *Echinochloa*, *Crus-galli*, *Euphorbia*, *Glycirrhiza*, *Epilobium*, *Rhus glabra* and the "sand-plum," probably *Prunus pumila*. "An inspection of the enormous pad of "hair, 4 to 12 inches long, that clothes the buffalo's (bison's) head from the "root of the horns to the muzzle, besides the dense long hair which clothes "the legs and breasts of the animals, reveals masses of hair matted with mud, "seeds, twigs, Cactus fronds and roots. In examining the heads of the dead "buffaloes, I repeatedly noticed in the long hair of the forehead capsules "of *Martynia* (*Proboscidea*), with seeds of *Bidens*, *Glycirrhiza*, *Stipa*, *Setaria*, *Elymus*, "seeds and pappus of *Helianthus* and other unknown *Compositae*, hispid twigs of "*Euphorbia*, and seeds of some species of *Rhus*, probably R. *trilobata*, seeds of "*Obione canescens* and of *Amaranthus* or *Chenopodium*."

This account gives a very good idea of the amount of transportation of seeds which is effected by the large hairy wandering mammals. During Pleistocene times the European bison was as abundant (to judge from palaeolithic drawings) in Europe as the American bison was in the early days of America, and probably rambled across Europe in the same way, transporting seeds from one place to another, and, besides it, the woolly mammoth and rhinoceros doubtless carried seeds in their long hair.

A certain number of the plants found along the track of the bison might have been eaten and the seeds passed in the excreta, such as *Amaranthus*, *Thlaspi*, *Trifolium*, *Setaria*, etc., but some, *Bidens*, *Glycirrhiza*, and *Proboscidea*, are specially adapted for adhering to the hair of such animals, while others, *Obione*, *Amaranthus*, *Rhus*, must simply have adhered to the animals' heads in mud.

This system of transport of seeds in mud, or attached by mucilage, or merely by wet, has doubtless been of the greatest importance to plants which have had no special adaptation for dispersal other than their small size and tendency to stickiness. The turf of small sedges, *Scirpus*, *Lipocarpa*, etc., and grasses like *Isachne*, which one finds traversing the forests, is probably formed by the dissemination of the small fruits of these plants on the feet of elephants, rhinoceros, etc., which utilise these paths, as much as by their swallowing the seeds with the foliage when browsing.

PORTIONS OF LIVING AQUATICS TRANSPORTED BY BIRDS, BATRACHIANS, ETC.

Some of the aquatic birds—ducks, moorhens, coots, etc.—frequently carry off portions of water-weeds, among which they have been diving or swimming, entangled round their necks or legs, or, in the case of Duckweeds (*Lemna*), merely adhering to their feathers, and in their flight may bear them to other pools or rivers. The distance to which they can carry these in a fit state to continue their growth is not very great, as in most cases the plant would soon become detached and fall off, and in any case, in a long flight, would dry

up and perish before the bird reached the next piece of water. In areas where pools and rivers are abundant and not too far apart, as in parts of India, Africa, and in any country where rice-fields are plentiful, a plant might be thus carried very speedily across the country. Most of the submerged water-plants are readily propagated by detached portions of the stem, and the *Elodea canadensis* owed its rapid dispersal over Europe entirely, or almost entirely, to this dispersal by vegetative fragments. Coots have been seen carrying portions of the stems of a *Potamogeton* around their necks as they flew. An anonymous writer in the *Morning Post*, February 13th, 1923, writes as follows :—" How " closely the flora and fauna of a park are connected is shown by some notes " made by the historian of Greenwich Park about plants introduced, even " seaside plants, by the birds. They brought the pretty water *Ranunculus* " as well as the unwelcome American Weed. The feet, feathers and food of " such birds as the lesser grebe, moorhen, kingfisher and teal, account for new " aquatic plants." The kingfisher as a plant transporter may, I think, be left out of account, as it never really immerses itself, but one or other of the birds mentioned must have been the carrier of the American Weed (*Elodea canadensis*) " over the park wall " in the form of fragments of the plant around its neck or legs, as it has never been known to fruit in southern England, and the water *Ranunculus* probably came in the same way.

Elodea canadensis (*Anacharis alsinastrum*).—This, the Canadian or American Weed, was introduced accidentally into England, probably more than once, from America. It is a slender submerged plant with long brittle stems covered with narrow leaves, any piece of which will grow when dropped into water.

In Europe it first appeared in Ireland at Dublin, where it was noted in a pond with introduced *Aponogetons* and other plants, and again at Waringstown, County Cork, in 1836. It then appeared in a pond at Dunse Castle, Berwick, in 1842, and spread thence to the River Whitadder. Before 1847 it seems to have been introduced to Foxton, Market Harborough, Leicestershire, in timber from North America. In Hampshire C. Babington writes :—H. Collins says it was introduced into a pond with roots of *Nymphaea odorata* from North America. It was not seen in the pond before these plants were introduced. It is quite possible that in these cases the plant came as seed in the cracks of the timber, and in the mud on the water plants, or it might have been used as packing material for the latter. Anyway, it appears to have been accidentally introduced into the British Isles twice at least. The plants introduced, for many years gave only female flowers. Male flowers first appeared in Edinburgh, 1879. It spread with great rapidity over rivers, canals and ditches (often choking them up), all over England and Scotland, and eventually crossed to France, Belgium (1860), Holland (1861), Germany, Denmark and Sweden, Russia and Hungary; but Arthur Bennett, writing in 1893, says it had gradually been becoming more rare for the past 20 years. At one time ditches were full, but now one has some difficulty in finding a specimen.

It is probable that it very rarely, if ever, was propagated in Europe by seed, but any small portion of the stem grows with great rapidity, much more so than in America. Asa Gray says : " As it occurred not only in streams, but " isolated ponds and lakes, and succeeded in crossing the Channel, it seems " almost certain that much of its migration was due to small pieces of it being " carried by ducks, coots, moorhens or grebes." Woodruffe-Peacock (in *Selborne Mag.*, xxviii, p. 98) writes :—" I only heard this morning of the " discovery of *Elodea*, duck-carried most certainly to an isolated pond in " Cumberland," and the historian of Greenwich Park, as stated above, says that it was brought over the park wall to the ponds by lesser grebe, moorhen or teal. I have experimented with this plant to discover how long a fragment of it would remain out of water and recover when re-immersed. A portion was

laid on a feather from 9.30 a.m. to 10.30 a.m., and although quite dry then, recovered very shortly after being restored to the aquarium. I then put it again in the open air for 23 hours, and by the next day it had quite recovered. Thus a duck might carry a bit on its feathers, flying at the rate of 40 miles an hour, for 920 miles and so disperse the plant.

Blyxa is an aquatic with a rosette of long narrow grassy leaves, and is stemless. It grows in comparatively shallow water, rice-fields, and *B. malayana*, in the lake in the Singapore Botanic Gardens, grew only in the shallow parts near the edge. The seed is papillose only in this species. The papillae may serve to attach it in mud to the feet of birds and also act as an anchor in mud. In *B. echinosperma*, of India, the seed has long spinous points. *B. malayana* was doubtless introduced into the Singapore Gardens artificial lake by its seeds, and probably by the duck, sandpipers, jacanas, or small herons which visited the lake from time to time.

Lagarosiphon is a tropical genus resembling and allied to *Enhydrias* and *Elodea*, and is widely spread in Africa and Asia. Mr. Burtt-Davy tells me that in a natural rain pond in the Transvaal, which was dry for 5 months in the year, there appeared suddenly some quantity of *Lagarosiphon muscoides*, which might have been brought by birds from the Vaal River, some distance away. This rain pond was constantly haunted by wild ducks, geese, flamingo, heron, ibis, and various waders. It was interesting to note that a submersed *Utricularia* (*U. stellaris*) appeared with it, recalling the appearance of *Utricularias* in the Singapore Gardens lake with *Enhydrias*. There can be no doubt that the whole of this style of floating long-stemmed aquatic plants, *Hydrilla*, *Elodea*, *Lagarosiphon*, *Ceratophyllum*, *Potamogeton*, etc., owe much, if not most, of their wide dispersal to their clinging to the legs of water-birds, though the attachment of their seeds to the feet or feathers and drifting in rivers and floods also help to account for the extraordinarily wide and rapid diffusion of these aquatic plants.

Hydrocharis morsus-ranae.—Guppy says of the Frog-Bit that the seeds sink in water, and one would hardly regard them as being able to stand a bird's digestion. When the fruit bursts, the gelatinous pulp containing the seeds is discharged, part of it sinks slowly, while some of it adheres to the outside of the fruit. This material would be very likely to adhere to the plumage of birds sitting on the water, and, in drying, the seeds would be firmly attached. This is quite possible, but evidence that it is actually so carried about is desirable. It is typically a ditch or pool plant, and it is difficult to see how it gets about. Mrs. Arber says it does not fruit in England, but is propagated by bulbils here, which sink and remain in an erect position.

Ottelia alismoides, a rice-field and pool plant in tropical Asia and Japan, probably gets carried about from one field to another by birds in the same way as Guppy suggests for *Hydrocharis*. Jozo Makajuma says that in Japan the fruit floats up to the top of the water and disintegrates, discharging its seed.

Callitriche is a small genus of aquatics very variable in foliage and length of stem, mostly found in pools and lakes, and one species on moist ground (*C. peploides*). One set, floating on the top of the water, has rather broad ovate leaves, (*C. verna*, etc.). Another set has a long submerged stem with linear leaves, and inhabits deeper waters, while the terrestrial one and some tidal-mud species form little round tufts with small leaves. The seeds of all, as far as known, are solitary in very small axillary fruits, and are said, both by Guppy and Praeger, to sink in the water immediately. Still, these plants are very widely dispersed even in distant oceanic islands. The surface-floating *C. verna* and the tufted tidal-mud *C. obtusangula* are certainly spread to some extent by water flow, but the presence of *C. verna* and the submerged species occurring in isolated ponds and lakes cannot be so accounted for. I have described, under

dispersal in mud by horses and cart-wheels, the conveyance of *C. verna* into puddles and ruts in Redlands Wood, Surrey, and there is no doubt that in many places it is conveyed on the feet of animals. But under the flora of isolated ponds it will be seen that it, and allied species, must be carried by birds, either as small pieces, or bulbils, or as seeds to various lakes (p. 546).

Many of the long-floating submersed species are found in deep water in lakes in Scotland, the Lake District, Wales, etc., where the plant could only have been brought by birds. Added to that we frequently have species inhabiting wet places in various oceanic islands. The genus is practically confined to cool and temperate regions, or cool spots in mountains in the tropics, Europe, North Africa, Abyssinia, Kenya, temperate Asia to China and Japan, India, Himalaya and Nilgherries, Australia, New Zealand, and North and South America. *C. verna* occurs in the Faroe Islands, Azores, Madeira, and Canaries; and *C. antarctica* in Marion, Kerguelen, Heard, Amsterdam, Lord Auckland, Hermite Isles, Falklands, Macquarie Isles, Kermadec, and South America. A species is also found in Madagascar. In these island plants the seeds may have been brought by wandering birds in mud on their feet or feathers. They are all of the same type as *C. verna*, with floating rosettes of leaves readily detached from the main plant, which might as easily adhere to the breasts of water-birds as *Lemna* does.

Potamogetons.—Many, if not all of these water-weeds grow very readily from fragments of the stem, and are undoubtedly carried to some distance by water fowl.

Woodruffe-Peacock writes thus (*Selborne Mag.*, xxviii, 99):—"I remember "watching the dew-pond at the foot of Sidbury Hill, on Salisbury Plain, in "August, 1889. I watched through field-glasses a pair of wild ducks "approaching the dew-pond. I saw them long before they reached the "water, and the drake had a necklace of pondweed, *Potamogeton perfoliatus*, "round its neck. I judged this plant to be about 3 feet long. Only once in "my life have I seen a duck carrying a larger fragment of this genus. It "was while watching at Ashby Decoy, many years ago. It was either a piece "of *P. praelongus* or *P. perfoliatus*—at this distance of time I cannot say which "species. I have often seen ducks carrying fragments of water plants on "their backs or round their necks. Twice, when shot in flight, the pieces "have turned out to be *Elodea canadensis*, once another pondweed, *Potamogeton* "*crispus*."

"Most water plants are carried about as wet seeds sticking to the head, "neck and back-feathers of ducks, according to my brother's observations." He came to the conclusion that, in the autumn, seeds on the back of diving birds were not infrequent, if they were sprung at diving or after diving or bottom-feeding operations, but were very rare after preening, cleaning and sleeping times. Now, ducks, he says, always come to their homing ponds for preening and cleaning labours, so they arrive from their night feeding or from other ponds, when disturbed early in the day, in an ideal state for carrying seeds to fresh places. I myself observed that the fruits of the very widely distributed *P. lucens* float freely on the surface of the water for the whole winter, and would easily adhere to the breasts of swimming birds.

Characeae, the Charas (*Nitella*, *Chara*, etc.) are an extremely widely and rapidly dispersed group of water-plants, distributed over the whole world, including many remote islands. They are plants of a very early epoch, fruit of them having been found in the lower oolite rocks, and through secondary and tertiary periods to the present day.

The plants are always submerged, and often very deeply, but are also met with in shallow water. They are very fragile, and fragments of the plant grow readily. The plants may be distributed by river and flood action to

some extent, but as they are pool or stagnant water plants rather than inhabitants of streams, this method of dispersal is probably not an important one. There is little doubt that the very wide dispersal of these plants is due mainly to the transport of their fruits, which are very minute, by birds and by some of the larger mammals, to whose feet the fruits adhere when trampled on in the mud, though portions of the plant itself may also be attached to animals and so be transported. According to Groves, Dr. Allen states that *Charas* also produce bulbils, which are eaten by ducks. Though they may be dispersed by fragments adhering to the body or feet of birds, it is more probable that they are dispersed mainly by their fruits.

Groves (in "British *Charophyta*") says that newly-made pits, such as those excavated from gravel and clay, are, at an early stage of their existence, also very favourite habitats for *Characeae*, being often carpeted with one or other of the common species, to the exclusion of other plants. In many cases, no doubt, the fruits or portions of the plants are carried to these spots on the feet of horses, or of cattle drinking at the pool, but in the larger ponds by birds, such as ducks, grebes, or moorhens.

Mr. Burtt-Davy informs me that in an artificial lake in a farm in the Transvaal, a species of *Chara* suddenly appeared. The specimens were lost, but it was probably *C. contraria*, which grew among stones in the Klip River, 3 miles away. This lake, a large piece of water, was constantly visited by ducks, geese, flamingos, ibis and herons, besides waders.

Among the aquatics in the artificial lake in the Singapore Botanic Gardens *Chara gymnopitys* occurred in great abundance. It has been found also in rice-fields and ditches in Johor and Perak, but has not yet been found elsewhere in Singapore. It is a native of Japan, Tonkin, Arracan, Australia and New Zealand. There can be no doubt that it has been brought by wandering birds, such as teal, cormorants, jacanas, blue heron or sandpipers, which constantly visited the lake.

In one of the Lankawi Islands, Dayong Bunting, is a deep lake among the limestone rocks, where a stream runs down to the sea, but, owing to its being blocked by a large limestone hill, the water can only escape slowly by an underground passage, thus forming the lake. Here Mr. Curtis found an abundance of *Chara flaccida* var. *brevibracteata*. He notes that the bottom of the lake must be a perfect cushion of this *Chara*. Such streams as flow into the lakes in these small limestone islands are too shallow and rapid for the growth of any aquatic vegetation; the variety that we find in this lake is known from Bengal only. The typical *C. flaccida* is found in Africa, the Marianne Isles, Celebes and Borneo.

Nitella opaca is recorded (in Wheldon and Wilson's "Flora of West Lancashire") as the first plant to have appeared in the Garstang Pond, dug for the purpose of discovering what aquatic or riparian plants would appear, and carefully fenced in to prevent the access of cattle. The only water-fowl known to visit the pond was the moorhen.

N. cernua.—In the oceanic island of Fernando de Noronha, 161 miles from the cost of Brazil, a volcanic island which, so far as is possible to make out, has never had any connection with the mainland, the expedition of the author, Messrs. T. S. Lea and G. Ramage, found in the interior a large lake or pond entirely filled up with a mass of *N. cernua*, a native of the West Indies. The mass was so dense that it was impossible to swim in the lake. There was no other aquatic in the lake, but in the weed was a water-snail, *Planorbis*, which was no doubt brought to the lake on the foot of some duck or other swimming bird in a young state, as Darwin has shown that just hatched freshwater molluscs crawled on to a duck's foot suspended in the water and survived in damp air for from 12 to 20 hours. During this length of time the duck might fly at least

600 or 700 miles, and, if blown across the sea to an oceanic islet, would be sure to alight on a pool or rivulet (" Origin of Species," xiii). We saw no ducks on Fernando de Noronha, but towards the end of our stay some waders (*Charadridae*), a plover, and a bird like a yellowshank were seen; evidently the migrants were just beginning to come as we left. Anyway, whichever bird brought the *Planorbis* could very well have brought the *Nitella*, either as a fragment or a fruit. A species of *Tolypella*, *T. antarctica*, and *Nitella Hookeri* occur on Kerguelen; *Chara gymnopus* in the Bermudas; *Ch. foetida* in Malta; *Ch. fragilis* and *Nitella hyalina* in the Azores; *N. Gibbsiae* and *N. gracilis* and *Ch. flaccida* in the Fiji Islands; and *Ch. gymnopus* in Hawaii. The transport of *Nitella microcarpa* by a rhinoceros is detailed under dispersal in mud attached to the feet of animals.

Characeae are absent, however, from most oceanic islands, but perhaps this is due rather to the usual absence of lakes and pools there than to anything else. Still, it is remarkable that none are recorded from Juan Fernandez, the Galapagos, and Canaries.

It is difficult to say, in cases of the transportation of these plants to long distances, whether they have been carried as fragments of stem or as fruits. I have, however, experimented with a species of *Chara* to see how long the plant would remain out of the water without being killed. I found that on placing a portion on a feather at 9.30 a.m. it was quite dry by 10.30 a.m.; re-immersing it in water, it was quite recovered and in good condition the next day. When kept out of water for 23 hours, only the terminal buds recovered.

The Duckweeds (*Lemnaceae*) and *Azollas* owe a good deal to birds in the matter of dispersal. Many ducks feed largely on *Lemna*, and, while doing so, these little plants adhere to their heads and backs, and may be borne for some distance. A pond on the outskirts of Reading was full of *Lemna minor* and *Azolla*, the latter an escape, no doubt due to wild-fowl (probably moorhens) from a park near by, where it had been introduced. I saw a moorhen running in an intermediate field between this pond and a very much smaller drinking pond for cattle; and this pond, ¼ mile away, contained both *Lemna* and *Azolla*. Woodruffe-Peacock (*Selborne Mag.*, xxviii, 1917, 98) mentions *Lemna minor* as occurring in a dewpond frequented by wild ducks, and it is certainly conveyed short distances in occupied country by tame ducks, as well as by running water.

In Singapore the Chinese cultivate, in small artificial ponds, *Pistia* and other aquatic plants for pig food, and in carrying these about in pails from village to village, frequently carry *Lemnas* and *Azolla* with them, and from such ponds these plants often drift down ditches connected with them, or are carried by their ducks, wandering down the ditches, often to the rice-fields.

In the Malay Peninsula and Sumatra, *Lemnas* are usually to be found in ditches or rice-fields, where tame ducks often go.

That *Lemna* can be carried by water-fowl to some distance is shown by Duval-Jouve, who found plants on the breasts and feet of wild-fowl in the French markets. I have not seen any in isolated ponds or lakes far from cultivation, such as the Welsh or Scotch lakes. They seem also to be markedly absent from distant islands, e.g., Fernando de Noronha, where there was a lake which, as previously stated, had almost certainly been visited by wild ducks; *Lemna minor* and *L. trisulca* occur in the Bermudas, but are not recorded till 1872; they are not mentioned in Michaux's account of Bermuda plants in 1806, but by 1872 there were many introduced European plants in these islands. They also occur in St. Helena, and are considered to be indigenous by Hemsley, but this seems to me very doubtful. Species occur in the Canaries, Cuba, and Jamaica and Porto Rico, as in the Fiji Islands and Galapagos, but

all are widely-distributed species, and it seems to me quite possible that these were accidentally introduced by man.

Guppy states that the seeds of the *Lemna minor* float in water, but I should doubt if any *Lemnae* are disseminated to any extent by the seed, as it is comparatively rare that any of them produce flowers, and, indeed, in some species flowers have never been seen. They seem usually to flower when the pond dries up. The seed might then be picked up by the feet of a wader or duck, and so be conveyed to a great distance, but the plants are probably diffused almost always in the vegetative form. To find out how long they would remain alive, after removal from water, I exposed *Lemna minor* on a feather in the open air for 12 hours. The fronds then appeared to be quite dried up, but recovered completely in a few hours in a tumbler of water. Other fronds survived 22 hours, but recovered more slowly. This period would be long enough to allow a duck to fly for a very long distance. Estimating the rapidity of its flight at only 20 miles an hour, it could carry the plant 440 miles. It will be seen (in the section on isolated ponds, p. 546) how frequently the *Lemnas* are conveyed about by birds, and in some cases by mammals.

Lemna aequinoctialis, of tropical Africa, is, as Dr. Welwitsch notes, an annual, drying rolled up in mud and developing very rapidly in the rains. It is a very small species, and could easily be transported in mud on the feet of birds or on those of larger mammals.

Wolffia arrhiza.—This very tiny duckweed, the smallest of flowering plants, usually occurs with *Lemna*. It is very widely spread over the world and remarkably sporadic, appearing in considerable abundance in a locality in some years, and then disappearing again. I have seen it on one occasion in abundance in a well in the Residency Gardens at Malacca ; in a year or two, when I revisited the spot, it had entirely disappeared. It has also been recorded from a well in Cairo. It is not possible that the plant could have been brought into the wells by wild-fowl, which would not go there, but it might have been brought by frogs or toads, which constantly fall into wells.

Weddell (*Ann. de Sc. Nat.*, ser. iii, Bot., t. 12, 1849, p. 155) writes that he shot in Brazil a water-fowl called " Camichi," of which the feathers were soiled with greenish matter, which he found to be *Wolffia braziliensis*.

Azolla.—I have already given an account of these little aquatics as dispersed by river and flood (*see* p. 179). I have only to add here their dispersal by birds and batrachians. They may be attached to the feet or feathers of water-birds. There is some evidence of this occurring in England, but it is more likely to be a common method of dispersal in India, Africa and Australia, where water-fowl are more abundant, and the climate more suited for its growth. In many cases it has been met with in isolated ponds and ditches not connected at all with streams and rivers, and it is impossible to see how it can have got to such spots except by the aid of birds. Saccardo says it has been largely spread by human agency, by birds, frogs, and in fishermen's nets, and that it appears in rice-fields treated with guano in Italy, whence the people call it " grassa del Guano." It certainly prefers stagnant or slow-moving water, though it is clearly dispersed by rivers and other flowing water. I have seen specimens at Kew recorded from a pond 2 miles from Haileybury College; on a small stagnant piece of water in Bournemouth; pond at Petersfield; Chigwell Pond; and water in old clay pits in Buenos Ayres. In these cases only water-fowl, or possibly batrachians, can have transported it. Near Reading I found a small isolated pond in a field containing this plant. About ½ mile away was a cattle pond in which it was very abundant, together with *Lemna* and *Ranunculus aquatilis*. A stream ran to this pond, and at some distance (a mile or so) was the Bulmershe Lake, where *Azolla* had doubtless been introduced, as it was plentiful. The small isolated pond contained *Ranunculus aquatilis* and *Elodea canadensis*, besides a

few plants of the *Azolla*, which, however, later disappeared. In this field I have seen moorhens going to a small pond from the larger one, and there can be little doubt that they carried the aquatics to the small pond.

Azolla may be carried about by water-birds, either by its fronds adhering to them or its spores, though, as it rarely, if ever, fruits in England, it is doubtless carried whole here, as *Lemna* is. The plants also produce winter buds, which, sinking into mud, may be carried on the feet of birds. I have kept these winter buds in a small pellet of mud quite dry for 2 days, and the plants, when placed in water, again recovered; but the plant itself will not survive 7 hours' drying. Hence, no doubt, its absence from distant lakes and pools and from oceanic islands.

Azolla and *Lemna* Dispersed by Batrachians.—Though the batrachia do not wander to long distances, they contrive to get from place to place, and therefore they are abundant in most parts of the world. Most of them are insectivorous, but they do transport such plants as *Azolla* and *Lemna*—which float on the water—by the adhesion of these plants to their bodies. Mr. A. P. P. Keep found one day, in a sunken bath in his garden on Holmwood Common, numerous plants of *Lemna minor* which had suddenly appeared, and at the same time a Newt (*Triton*) also appeared in the water. I sought in vain in the neighbourhood for *Lemna*, nor did I see any newts in the ponds. I could only conclude the newt must have come from some distance, and brought the *Lemna* adhering to it. E. Chateau (in *Antun Bull. Soc. Hist. Nat.*, 21, 1908, p. 76), describes a somewhat similar transportation of *Azolla caroliniana* by toads. He kept the *Azolla* in pots of water in his garden, and, finding some of the plant thrown out on the ground, examined the pots at night, and found two large toads and a green frog in the water among the *Azolla*. When they went off, they carried off a quantity of the plant, and conveyed it to a horse-pond in a meadow 200 metres away. Later he found a very large toad in the *Azolla* pans, and when he drove it away, it went to a pit where later the plant was found to be growing. Under *Wolffia arrhiza* I have mentioned already the probable action of frogs and toads in transporting this minute aquatic. The slow wandering of these batrachians may in time transfer these floating aquatics to a considerable distance, and may help to diffuse the plants over areas as considerable as frogs and toads themselves occupy, though doubtless water-birds effect the dispersal more readily and to greater distances.

SEEDS AND SMALL FRUITS TRANSPORTED ON THE FEET OF BIRDS.

The carriage of seeds on the feet of birds in mud was first called attention to by Charles Darwin (in the "Origin of Species," chap. xii). He states that he removed 61 grains, and 22 grains, of dry argillaceous earth respectively, from the feet of 2 partridges, and in the earth was a pebble as large as the seed of a Vetch. The leg of a woodcock was sent to him by a friend with a little cake of earth attached to the shank, containing a seed of *Juncus bufonius*, which germinated and flowered. (This plant is a very widely spread one, which occasionally appears by isolated ponds.) He cites Mr. Swaysland, of Brighton, who informed him that he had often shot wagtails, wheatears, and whinchats on their first arrival on our shores, and has several times found little cakes of earth adhering to their feet.

Prof. Newton sent the leg of a Red-legged Partridge (*Caccabis rufa*), which had been wounded and could not fly, with a ball of hard earth weighing 6½ ounces, and measuring 7½ inches round. It is figured in Stevenson's "Birds

of Norfolk." The earth had been on the bird's leg for 3 years, but, when broken and placed under a bell-jar and watered, no less than 84 plants sprang from it, consisting of 12 *Monocotyledons*, including the oat and one other kind of grass, and 72 *Dicotyledons* of at least 3 distinct species. Marsh mud, as he shows, abounds in seeds, and these may be conveyed from marsh to marsh and pool to pool by water-fowl.

Sir Baldwin Spencer (in " Wanderings in Wild Australia," i, 21) writes :— " I saw one of them (a miserable crow) fly away with a good-sized pellet of " mud fastened to one of its legs. We were camped by a muddy waterhole, " with a few crows perched on dead trees. If there were any little snail or " crustacean, or even fish eggs in it, they would as likely as not be left behind " in some waterhole miles away." Birds fly from whatever kind of ground they frequent to a similar spot without stopping. A bird such as a redshank flies from one marsh to another ; mountain birds fly along mountain ranges to more distant ones, and rarely, if ever, descend to the plains. The marsh bird, therefore, brings the seeds of marsh plants to the marshes only, aquatic birds bring those of water-plants to pools or rivers, and so on.

They do not commonly stop on dry ground and so dispose of the seeds they convey on soil useless to the plant. Naturally the birds which can convey seeds in this manner are birds which habitually run along the ground, such as partridges and pheasants ; and especially important are the *Charadridae*, snipes, woodcocks and sandpipers, as also ducks, which stand and walk in mud by streams and pools.

Seeds so conveyed must be small, such as the seeds of *Polygonums*, sedges, grasses, etc., and this method of dispersal probably accounts for the very wide distribution of some of the sedges, and especially such plants as *Polygonum hydropiper* and *P. minus*. These are two of the very few flowering plants common to Europe (England) and the Malay Peninsula. They are not weeds of cultivation brought by man, as they do not grow in cultivated land but by the sides of streamlets too narrow and shallow for ducks to visit, but are the favourite haunts of the sandpipers.

The *Charadridae*, snipes, woodcock and sandpipers form a very large group of wading birds which usually nest in Siberia or other parts of the temperate zone, and migrate in vast quantities to immense distances. With the exception of a few species (the grey and green Plovers (*Squatarola*), etc.), the *Charadridae* feed entirely on worms, insects, and mollusca. The distances to which they migrate are much further than those of almost any other land birds. Thus the woodcock, snipe, common sandpiper, black-winged stilt, ruff, grey plover, curlew and whimbrel, all birds of the north temperate zone, fly as far south as the Malay Peninsula, and some as far as Java, and they have no trouble in crossing long stretches of sea. I saw several of these wanderers in Fernando de Noronha, and some reach Christmas Island. In the Botanic Gardens in Singapore there was a large artificial pond which was visited regularly by Sandpipers (*Tringa*), and at spots where they habitually rested, there appeared *Rhynchospora aurea*, *Heleocharis capitata* (quite a scarce plant, and only known in the island from one other locality) and *Eriocaulon sexangulare*, all plants which did not occur near enough to the lake to be accounted for in any other way. Teal (*Dendrocygna javanica* and *Nettopus coromandelianus*), jacanas, and small blue herons also haunted the lake from time to time, and might be responsible for the presence of some of these marsh plants, and the aquatics *Enhydrias*, *Blyxa*, *Naias*, *Utricularia* and *Nitella*, of which the lake was full. Besides the above-mentioned birds, we must add the storks, rails, and many sea-birds as seed dispersers of this nature. I give elsewhere notes of birds conveying seeds and fruits of an adhesive nature, either due to spines or hooks or viscid exudation, but they certainly also transport seeds and small

fruits picked up in mud on their feet and feathers, such as are unprovided with any adhesive apparatus.

Kerner states that he examined the mud taken from the beaks, feet, and feathers of swallows, snipe, wagtails and jackdaws, which birds take very long flights (wagtails habitually fly from Java to Christmas Island), and he found seeds of a considerable number of species embedded in it. He mentions the following, many of which are very characteristic of isolated pools: *Glyceria fluitans*, *Cyperus flavescens* and *C. fuscus*, *Heleocharis acicularis*, *Isolepis* (*Scirpus*) *setaceus*, *Scirpus maritimus*, *Juncus bufonius*, *J. compressus*, *J. lamprocarpus*, *Limosella aquatica*, *Lindernia pyxidifera*, *Samolus Valerandi*, *Centunculus minimus*, *Veronica anagallis*, *Erythraea pulchella*, *Glaux maritima*, *Lythrum salicaria*, *Elatine hydropiper*, *Nasturtium palustre*, *N. amphibium*, *N. sylvestre*. The association of many of these herbs with isolated ponds will be noticed in the section dealing with them (p. 546).

Of these plants, Kerner remarks that most are distributed over all parts of the world, but are seldom found to remain long in any particular locality. They often start up quite unexpectedly at places where migrating birds have gone to drink.

"The extraordinary occurrence of the tiny grass *Coleanthus subtilis* on "the edges of ponds in Southern Bohemia (1852) and Southern France (1863), "in Austria, and in the Tyrol, may be unhesitatingly attributed to this method "of dispersal, as may also be the occurrence of the subtropical *Heleocharis* "*atropurpureus* on the shores of the lake of Geneva, and of the *Anagallis* "*tenella* on the shores of the Schwarzsee and Kitzbuhl, in Northern "Tyrol." Nearly all the plants he mentions are typical pond-edge plants, and "it is to such spots that swallows resort to gather mud for their "nests, wagtails in search of insects, and the snipe and jackdaw for food "or water."

The occurrence of the seeds of Rushes (*Junci*), the small *Cyperi*, and *Heleocharis*, is important, as these are very widely distributed, and yet, except in this manner, seem to have no adequate methods of dispersal for long distances. Kerner also calls attention to the fact that many seeds of aquatic plants float, instancing those of *Alisma*, *Carex*, *Myriophyllum*, *Phellandrium* (*Oenanthe*), *Polygonum*, *Potamogeton*, *Sagittaria* and *Sparganium*, and that water-fowl rising from the water may bear them off merely attached to their feathers by the wet.

Duval-Jouve, in his letters to M. Schoenfeld on the occurrence of *Coleanthus subtilis* in Brittany and the Tyrol, referred to above, states that he has often examined dead game-birds in the market, and has found, almost always, fruits and seeds adhering to their breasts and feet, mostly on the feet. He has noted among them fruits of *Alisma plantago* and *Echinodorus ranunculoides*, seeds of *Juncus* sp., *Glyceria fluitans* with glumes, and twice *Lemna*.

Meister, in writing of *Utricularia*, says that when the seeds fall from the capsule they float on the water and are dispersed by wind, and he thinks that birds carry the seed and the winter bulbs on their feet; but I believe they also carry fragments of these plants on their legs. These instances of seeds and small fruits, especially of marsh, pool and riverside plants, are sufficient to establish the fact that very many of such plants can owe their wide distribution to this action of birds, and this, indeed, is the only way in which the occurrence of such plants in and about pools can be accounted for. However, more actual examination of the feet, beaks, and plumage of these wandering birds is much required, and the attention of naturalist-sportsmen is called to this question.

Isolated Ponds and Distant Marshes.

A valuable study of the different floras of several isolated dew-ponds in various parts of England was published by Mr. Clement Reid (in the Trans. Norfolk and Norwich Nat. Hist. Soc., 1894). These ponds are formed by an accumulation of rain and dew, and have no connection with other bodies of water or streams. In such ponds, far away from other ponds or rivers, and not in such position that seeds can be brought on the wheels of carts or feet of horses and cattle, the only vegetation of flowering plants must be brought by birds, either in the form of fragments of an aquatic plant or by seeds or small fruits attached to their beaks, feet, or feathers. I have seen some such ponds which were never visited by water-fowl, and in these no such vegetation appeared at all over a space of many years, but where these wandering birds do come, the ponds are soon furnished with vegetation.

Clement Reid describes the contents of 3 dew-ponds :—

A.—Contained *Juncus*, not flowering, but abundant; *Potamogeton densus*, very abundant; *Ranunculus aquatilis*, *Chara* sp., *Elodea canadensis*.
B.—*Ranunculus aquatilis* and *Elodea*.
C.—*Potamogeton natans* and *Zannichellia palustris*.

Of these plants, the *Elodea* must have arrived as a fragment twisted round the leg of a water-fowl, and by the same method we may account for the presence of *Zannichellia* and *Potamogeton densus*, and possibly the *Chara*, but it is more likely that the seeds of that and the *Juncus* were borne on the feet of a bird in mud, and the *Ranunculus* and *Zannichellia* by the achenes attached to the feathers, though these again may have been borne by fragments of the stem attached to the leg of a bird. *Potamogeton natans* must have been brought by some water-fowl which had swallowed the fruit and passed the seed, as the plant is too bulky to be conveyed by attachment to a bird's leg, and the seed perhaps too large to be conveyed in mud on its foot, and it has no hooked adhesive stigma, as has the *Ranunculus*, to allow of its attachment to the plumage.

In other ponds he recorded the following :—

Nasturtium officinale only occurs in isolated ponds fed by springs. (The seed of this is reported not to float, but any portion of the stem will grow, so that it is probably dispersed by floating fragments.)

Myriophyllum spicatum and *Hippuris vulgaris* occur once, each in an isolated pond, seeds probably carried on birds' feet.

Callitriche.—One of the most abundant water-weeds, next only to *Ranunculus aquatilis*. (Fruits probably attached to birds' feet, but possibly also portions of the plant.)

Peplis portula occurs on wet floors of sand-pits, which, though surrounded by dry heaths, have been deepened till the water level has been reached, and so have their floors constantly moist.

Both species of *Bidens* have been seen on the edges of pools, but neither is common. (These plants I have often found beside distant pools, and conclude that they are carried by adhesion to the feathers of birds or perhaps the hair of mammals. I have seen them both on the edges of pools on Sheen Common, where it is hardly probable that water-birds come.)

Hottonia, *Samolus*, and *Menyanthes* occur in isolated ponds (probably brought by ducks).

Scrophularia is rare, and has not been observed in ponds far from other water. (The seeds of this plant sink in water, but germinate beneath and float as seedlings, as do those of *Mimulus*. These seedlings are not likely to

adhere to birds and be so dispersed, as they would probably not survive their transport.)

Mentha, *Lycopus*, and *Stachys palustris* are often seen in ponds railed in so that cattle cannot get at them, therefore these must be bird-transported. The aquatic species of *Polygonum* occur frequently on horse-ponds by the roadside, but are uncommon in dew-ponds in open downs (the nutlets are probably brought in mud on the feet of cattle and horses). *Rumex maritimus* was once seen by Clement Reid in an old moat, possibly brought by adhesion to clothes. *Ceratophyllum demersum* was only once seen, and *Elodea canadensis* three times, in ponds on open downs, both probably brought by adhesive fragments. Both the common species of *Typha* and *Sparganium ramosum*, more rarely *S. simplex*, are found in ponds inaccessible to cattle. The Reed Mace (*Typha*) perhaps had the seeds brought by wind, or they may have come attached to the plumage of birds. *Sparganium* fruit is swallowed and the seed passed by ducks. *Lemna* is common, though many of the more distant ponds are without it. (I have seen abundance in isolated small ponds in Richmond Park, possibly brought from other ponds by deer and cattle, but more likely by ducks, which certainly visit them.)

Alisma plantago is sufficiently common in old sand-pits.

The most common *Potamogeton* is *P. densus*. *Zannichellia* was seen twice only.

Clement Reid says he believes that *Carex pulicaris*, *C. paniculata*, *C. vulpina*, *C. glauca*, *Juncus communis* and *J. bufonius*, are all common. A few of the ponds in old quarries and gravel pits are full of *Chara fragilis*.

Wheldon and Wilson in the " Flora of Leicestershire " (in Arber's " Water Plants ") describes how a pond was dug and railed off from cattle at Garstang. After 15 months *Alisma plantago* and *Callitriche* and *Glyceria fluitans* appeared. After 5 more months the only addition was *Juncus communis*. The only water-birds seen there were moorhens.

Woodruffe-Peacock described a sipe-pond or plash on Scunthorpe, Warren, Lincolnshire, a pond often dried up. He visited it in 1910, and found the following plants there :—*Anagallis tenella*, *Galium palustre*, *Hydrocotyle vulgaris*, *Hypericum elodes*, *Juncus bulbosus* and *J. sylvaticus*, *Myosotis palustris*, *Myriophyllum spicatum*, *Samolus Valerandi*, *Potamogeton polygonifolius*, *Comarum palustre*, *Littorella uniflora* (only known on one other common in the district, and that the most duck-haunted spot in the country), *Nitella flexilis*, *Pilularia globulifera*.

All these plants, he says, he has proved over and over again to be duck-carried. Of them, the *Potamogeton* and *Comarum* were doubtless derived from seeds swallowed by the ducks ; the rest doubtless adhered to their feathers or feet. Among these plants is mentioned *Littorella uniflora* (*L. lacustris*), of which Stelfox (in the *Irish Naturalist*, 1922, p. 130) records the appearance in abundance in Glenasmole Reservoir, County Dublin. It was not known to occur here by Colgan, who collected at this spot in 1901, and it had presumably arrived since that date. Its nearest locality was Lough Bray, Co. Wicklow, which was 4½ miles away. It is extremely abundant on the shores of the isolated Dozmary Pool in Cornwall.

Another pond which Woodruffe-Peacock describes as having been apparently visited by ducks, contained :—*Glyceria fluitans*, *Nasturtium palustre*, *Ranunculus Drouetii*, *Lemna minor*, *Veronica Anagallis*, *Alisma plantago*, *Myosotis palustris*. The pond, however, was full of moss, and he did not see the ducks stop there in their flight. He adds that in the first-mentioned pond were the water-snails *Planorbis spiralis*, *Limnaea glabra* and *L. pereger*, and *Pisidium pusillum*. The last-mentioned is recorded as being dispersed by water-beetles, but the others by ducks (Darwin, " Origin of Species," xiii), certainly suggesting the former presence of ducks in that pool.

It will be noticed that several of these plants are remarkably characteristic of isolated ponds, e.g., *Glyceria fluitans*, *Chara* and *Nitella*, *Alisma plantago*, *Ranunculus aquatilis*, and *Lemna*, all known definitely to be carried by water-birds from one pool to another.

F. C. Gates (in "Establishment of Plant Association," *Ecology*, viii, 339, 1927) describes an abandoned sand-pit filled with water in Kansas, which was surrounded by plantless areas, though cornfields lay at some distance from it. In 1923 there was no vegetation, nor was there any in the spring of 1924, but in the summer of that year there appeared *Typha latifolia*, *Sagittaria latifolia*, and *Salix interior*. The *Typha* and *Sagittaria* grew no nearer than 1 kilometre to the south, the *Salix* ½ a kilometre. Coots and sandpipers visited the pits. The *Typha* and *Salix* may easily have been brought by wind, but the *Sagittaria* was probably brought on the feet or feathers of the birds.

I examined an isolated pond on the heath at Arne, Dorsetshire. I found in it *Potamogeton polygonifolius*, *Echinodorus ranunculoides*, and a *Chara*. On the pond was a little grebe, showing that this pond was occasionally visited by water-fowl.

The Silent Pool in Surrey, at the foot of the chalk hills near Albury, contained no phanerogamic vegetation except *Callitriche*. It is probably never visited by water-fowl.

To Prof. J. W. Heslop-Harrison I am indebted for some very interesting notes as to the occurrence of *Scirpus maritimus* in an inland marsh at Birtley, in County Durham. He writes :—" The marsh in question is of quite recent " origin, formed by the overflow of a burn being trapped in a field by a railway " embankment. There is a ridge 400 feet high between it and the sea, which " is 12 miles away. It has never been connected with tidal flats or the sea. " Moreover, there are no flats of that type with which it might have been con- " nected. I know of no locality for *Scirpus maritimus* nearer than the Tees " mouth, some 36 miles away, where it abounds in the salt marshes and fleets, " even in some freshwater fleets cut off from the sea by embankments made " over 200 years ago. The plant has been known in Birtley Marsh for at " least 20 years, seems quite at home, and is spreading. The marsh and the " salt-marsh area are the well-known haunts of endless wild birds, resident " or migrant—coot, teal, mallard, grebe, etc. No other maritime plants are " to be found in the marsh, but I have noticed the gradual increase in the " number of species of plants it possesses, *Echinodorus ranunculoides*, *Myosotis* " *palustris*, and *Hippuris vulgaris* being its latest arrivals, and I may add *Ranunculus* " *sceleratus*, which does occur in brackish water, and quite commonly at the " Tees mouth." It is quite clear that *Scirpus* at least must have been transported by some wild-fowl, as seed in mud on their feet, from the mud-banks of the Tees River, and in all probability the other marsh plants came in the same way.

Scirpus maritimus is a sedge of very wide distribution. It is found all over Europe as far north as Iceland, also in Morocco, Canaries, Azores, North Asia, India from Kashmir, Kashgar (at 10,000 feet altitude), to Malabar and Mysore, Assam, Burma, China, Japan, Formosa, Egypt, West Tropical Africa, New Zealand, Clarence Isle, Norfolk Isle and Hawaii, and Australia. It is absent from the tropics of both hemispheres. It is variously described as occurring in salt lakes, dried-up freshwater swamps, around ponds slightly brackish, muddy shores, river edges and tidal mud, and seashores. In many of these localities its achenes must have arrived on birds' feet. *Scirpus lacustris* is even more widely distributed, doubtless because it does not actually require brackish mud, and it can stand a good deal of salinity. It occurs all over Europe and temperate Asia, China and Japan, at one spot in the Philippines, Australia, New Zealand, Hawaii, New Caledonia and many Polynesian islands, South

Africa, North America, Mexico, Jamaica, Cuba, Bermuda. In a note in Kew Herbarium, Phillips writes of it :—" Memorable as growing out of a pool on " the seaside, when I was in search of water to the west of Arthur's Seat " (Australia), which seems to imply there was no river or large body of water in the neighbourhood. It occurs in Norfolk Island and in Easter Island. " Common in the craters of extinct volcanos " (Fuentes). It seems very probable that this plant must be carried to these isolated ponds in mud on the feet or feathers of water-fowl, as it is difficult to see how it could otherwise get to such spots as volcanic craters. Its distribution area seems to be chiefly limited by its intolerance of a hot climate.

I have already mentioned the lake in Fernando de Noronha which was full of *Nitells cernua*, and contained also a species of *Planorbis*, a freshwater snail whose dispersal is associated with ducks ; no ducks were known to frequent this pool, which was little known to the residents, but several waders haunted the island, and also the isolated lake of Dayong Bunting in the Lankawi Islands off the coast of the Malay Peninsula, which also contained great abundance of *Chara flaccida* var. *brevibracteata*, which must have been brought from a long distance by some water-fowl.

Praeger (in the " Survey of Clare Island ") states that he found near Frankford, King's County, Ireland, a colony of black-headed gulls which bred in the centre of a large peat bog, ½ mile from farm-land (which, no doubt, these birds often visited in search of food). The guano and trampling of the birds had destroyed the bog vegetation, and a coarse herbage had sprung up. It contained the following plants, undoubtedly brought by the gulls as fruits or seeds attached to their feet and plumage :—

Capsella Bursa-pastoris (mucilaginous), *Cerastium triviale* and *C. glomeratum* (adhesive), *Sagina procumbens*, *Trifolium repens*, *Epilobium obscurum*, *Daucus carota* (adhesive), *Bellis perennis* (mucilaginous), *Senecio vulgaris* (mucilaginous), *Hypochaeris radicata*, *Veronica Chamoedrys*, *V. arvensis*, *Prunella vulgaris* (mucilaginous), *Plantago major* (mucilaginous), *Atriplex* sp., *Polygonum persicaria*, *Rumex acetosella*, *Juncus effusus*, *Holcus lanatus* (adhesive), *Poa annua*.

It is interesting to note how many of these seeds and fruits are mucilaginous or have other methods of adhesion.

SMALL-SEEDED PLANTS IN ISLANDS.

Such plants as cannot (so far as I see) have been transported to remote islands otherwise than on the feet of marsh and seashore birds are those marsh and swamp plants with small seeds which possess no other means of dispersal adequate to account for their distribution. I give an account of some of these arranged in natural order : *Colobanthus diffusus* (St. Paul's Island) ; *C. Kerguelensis* (Kerguelen and Heard Island) ; *Stellaria cuspidata*, *Sagina chinensis*, *Spergularia rubra* (Juan Fernandez) ; *Lyallia* (Kerguelen and Marion Island) ; (*Caryophyllaceae*). *Cardamine* (2 species in Juan Fernandez, 1 also in Tristan d'Acunha) ; *Senebiera Heleniana* (St. Helena) ; (*Cruciferae*). *Montia fontana* (Kerguelen and Marion Isles). (*Portulacaceae*) ; *Tillaea moschata* (Kerguelen and Marion), *T. muscosa* (Azores) ; *Polycarpon tetraphyllum* (St. Helena, Tristan d'Acunha, Azores) ; (*Crassulaceæ*). *Mesembryanthemum cryptantha*, *Pharnaceum acidum* (St. Helena) ; (*Ficoideae*). *Haloragis* sp. (Juan Fernandez and Antarctics, absent from South America) ; *Hydrocotyle capitata* (Juan Fernandez) ; *Sium* (2 species) (St. Helena) ; *Azorella Selago* (Kerguelen, Marion, Heard Island) (*Umbelliferae*) ; *Galium antarcticum* (Kerguelen) ; *Hedyotis arborea* (St. Helena) (*Rubiaceae*) ; *Wahlenbergia* (*Campanulaceae*), (3 endemic in Juan Fernandez, 4 endemic in St. Helena) ; *Centunculus pentandrus* (Juan Fernandez), *C. minimus* (Azores), (*Gentianaceae*) *Heliotropium panneum* (*Boragineae*) and *Dichondra repens*

(*Convolvulaceae*) (St. Helena); *Limosella aquatica* (St. Helena); *Plantago robusta* (St. Helena), *P. stauntoni* (St. Paul), *P. pentasperma* (Amsterdam Island); *Littorella uniflora* (Azores) (*Plantagineae*); *Acalypha rubra* (St. Helena); *Euphorbia chamaesyce* (St. Helena), *E. mellifera* and *E. azorica* (Azores). The small-seeded *Euphorbias* seem to spread about the world very rapidly, getting constantly to islands in spite of their want of special adaptation for dispersal.

Alternanthera paronychioides (South Trinidad); *Juncus scheuzeroides* (Kerguelen), *J. tristanianus* (Tristan d'Acunha), *J. communis* (St. Paul, Amsterdam, Azores), *J. bufonius*, *J. capitatus*, *J. supinus* and several others; *Luzula purpureo-splendens*, endemic, and *L. campestris* (Azores) (*Juncaceae*); *Scirpus setosus* (St. Helena), *S. nodosus* (Juan Fernandez, St. Helena, St. Paul, Amsterdam), *S. lacustris* (Norfolk Island, Easter Island, common in craters of extinct volcanoes, Bermudas); *Scirpus* (4 species in Tristan d'Acunha, 1 in St. Paul and Amsterdam), *S. Savii* and *S. fluitans* (Azores); *Fimbristylis* (2 species in St. Helena) and many more (*Cyperaceae*). It will be noticed that a number of these little plants, such as *Montia*, *Hydrocotyle*, *Limosella*, *Littorella*, *Scirpus*, *Juncus*, belong to genera, and in some cases are the actual species of which we have distinct records of their attachment in mud to the feet of migrant birds, and transportation to isolated ponds and marshes. All the islands above-mentioned, sea-birds at least visit, and in many of them we know also that the wandering ducks, rails, waders and herons appear from time to time, and frequently are regular visitants. One cannot doubt that all, or nearly all, the above-mentioned plants owe their presence in the islands to these birds.

CHAPTER VII

DISPERSAL BY ADHESION THROUGH SPECIAL MODIFICATION

Portions of Plants Adhesive to Animals, Adhesion by Branchlets of the Inflorescence, Adhesion by Armed Bracts, Adhesion by Plumes of Grasses, Adhesive Perianth-Lobes, Adhesive Calyces, Adhesive Corolla, Adhesion by Hooked Styles, Spiny and Hooked Fruits, Adhesion of Seeds by Hooked Hairs, Adhesion of Bulbils—Plants Dispersed by Adhesion to the Wool of Sheep, Lists.

PLANTS which possess special modifications for dispersal by adhesion are, as a rule, only to be met with where there is a sufficient abundance of animals suitable for their transport. Cases, however, do occur when, for some reason or other, the animals have become scanty or altogether disappeared, though the plant persists. In such cases, however, unless the plant has some other means of dispersal, it ceases to spread, becomes what is known as local, or may disappear altogether. Jean Massart (in a "Voyage Botanique au Sahara," p. 122) puts this very clearly. He says: "On the borders of the Sahara, when one "gets up in the morning, one finds an infinity of fruits of annual plants "attached to the rugs. They are those of *Aegilops*, numerous *Medicagos*, "*Emex spinosa* (*Polygonaceae*), *Daucus pubescens* and other *Umbelliferae* indeter-"minable, *Compositae*, and finally *Sclerocephalus arabicus*, a *Caryophyllaceous* "plant whose indehiscent capsules are surrounded by strong bracts which "are armed with hooks. In the Sahara itself hooked fruits are of no use; "the mammals, to whose hair the fruits are destined to attach themselves, "are much too scarce, and the plants cannot reckon on their help for dissemina-"tion. We have seen in the desert only two fruits armed with hooks—"*Limoniastrum Feei* and *Neurada procumbens*. We may add *Forskahlea tenacis-*"*sima*, a woody *Urticacea*. Its branches disarticulate readily, and, as they are "furnished with stiff hooked hairs, they fix themselves in the hair of animals. "The fragments root when they fall on the ground."

Besides the fact, which Massart points out, that plants depending on dispersal by adhesion of their fruits to the hair of animals would not in the desert (where mammals were absent) be disseminated at all, and so die out, there is also the important fact that the animals outside the desert do not go there, and consequently would not carry the seeds there.

In fact, the presence of plants with adhesive seeds connotes the presence of abundance of mammals clad with hair, or to a less extent of birds, to which must be added man with his clothing, either at the present epoch or in the past; so that in the oceanic islands, uninhabited by man, only such adhesive fruits occur as can be brought by sea-birds.

The desert in which Massart made his researches was the Algerian desert south of Biskra, where mammals seem to have been entirely wanting. Buxton, who describes the fauna of another part of Sahara (in his "Animal Life in

the Deserts," p. 135), found a number of mammals inhabiting these sandy wastes, and says: "It is common to find such burrs in large numbers in the "coats of sheep, jackals, and even such smooth-haired animals as gazelles "and jerboas. Numberless examples of seed and seed-vessels armed with "hooks and spines could be quoted from the flora of the great Palaearctic "desert, especially among the annuals."

Such plants on the borders of the deserts as are armed with hooks for mammal dispersal can only penetrate the desert where mammals are absent, or persist after the mammals have disappeared, and where wind is the only dispersal agent, by becoming modified for wind-dispersal. Failing that, the species must disappear. Massart cites *Marrubium deserti* as an example. In nearly all the other species of this genus the calyx lobes are formed into hooks for attachment to mammalian fur, but in this species, an inhabitant of deserts, where mammals are scarce or wanting, the calyx limb is widely spread in the form of a parachute, so that the plant can be wind-dispersed. A study of the genus *Geum* shows much the same thing, but in a sense reversed. The Arctic and high mountain species have a plumed style which, persisting, forms a suitable apparatus for wind-dispersal. A bend or kink is formed about the middle of the persistent style, and above this, in the species inhabiting the lowlands, where animals are abundant, the style breaks off, leaving a hook which readily adheres to fur or clothing, and the plant is so dispersed. The Sea-Carrot (*Daucus maritima*) has spiny fruits, evidently destined for dispersal by adhesion, and is to some extent so disseminated; but it would not be so extremely abundant on our coasts as it is, if the fruits were not light enough to be wind-dispersed as well, and it is to this factor that it owes its wide distribution and abundance. When man appeared and, by hunting and agriculture, exterminated the wild beasts, he substituted the domestic cattle, sheep and goats, and the dog and cat for the wild mammals, and by the use of clothing also, replaced the former carriers of the adhesive seeds and fruits, and in many cases increased the area and abundance of the plants so disseminated. *Bidens tripartita*, *Galium aparine*, *Arctium Lappa* in the Cromerian days, and *Caucalis nodosa* of the Interglacial period, must have owed their dispersal in those days to the innumerable wild beasts of those periods, which are now extinct; but after the Pleistocene Age they were, and still are, disseminated by man and his domestic animals.

Agrimonia Blumei, of Java, still continues to spread along the roadsides of the cultivated area of Tosari in Java, though there are no wild mammals left there to carry its hooked fruits about, a few cattle or goats, and the sarongs of the natives, as they brush along the banks being enough to carry the plant further on, and the grasses *Chrysopogon aciculatus* and *Paspalum conjugatum*, by their adhesion to human clothing, have spread far more widely than they could ever have done by the aid of the wild animals of India and South America, their respective homes of origin.

Mammals and birds become more or less covered with burrs or other adhesive fruits by pushing through or settling in the branches of trees or bushes, or by walking on or lying down on the herbaceous plants provided with adhesive fruits. These attach themselves most readily to animals with woolly or long hair. Thus a spaniel or retriever collects more burrs than a smooth-haired fox-terrier. Sheep probably collect more of these fruits and seeds in their wool than any other animal. The loose-textured clothing of man also collects a large number, especially of the smaller kinds. The feathers of a bird, being more smooth, collect fewer, so that birds play a much smaller part in their dispersal than do the furry mammals. It is, however, to the birds that we owe the dispersal of the comparatively small numbers of viscid or hooked fruit in the oceanic islands, but it is no doubt due to the general

ineffectiveness of birds in this method of dispersal that adhesive fruits are mainly confined to low shrubs and herbs, which readily come into contact with wandering mammals. Animals do not usually notice the burrs that cling to them till they have ceased their wanderings and come to rest, when they remove and cast away the burrs with their teeth or claws. Hence it is very common to find plants of *Cynoglossum* at the mouths of the rabbit-burrows, where the rabbits, before going underground, have disencumbered themselves of the armed nutlets. Over open country the small burrowing rodents, rabbits, viscachas, marmots and susliks, and perhaps such animals as the fox and badger, collect a number of adhesive fruits and seeds of herbaceous plants, and disembarrass themselves of them at the mouths of their burrows on the loose turned-up soil, which is very suitable for the growth of these plants. At the mouth of rabbit-burrows we find nettles (*Urtica*), *Cynoglossum*, *Myosotis*, *Marrubium*, etc., and where the viscachas of South America dig are *Xanthium*, *Urtica*, and other such plants.

A. N. Formosov (in " Mammals in the Steppe Biocenose," *Ecology*, ix, 449) gives some account of the plants found growing on the mounds thrown up by marmots and susliks in Siberia. On those of the Marmot (*Marmota bobache*) he finds : *Salsola corallina*, *Thermopsis lanceolata*, *Axyris amaranthoides*, *Rheum* sp., *Urtica cannabina*, *Pyrethrum multifoliatum*, *Jurinea linearifolia*, *Serratula xeranthe-moides*, (*Compositae*) *Lepidium perfoliatum* (seeds mucilaginous), *Kochia striata*, *Festuca sulcata*, *Koeleria gracilis*, *Stipa Lessingiana*, *Bromus tectorum* and *Rochelia stellata*. Of these, *Urtica*, *Stipa* and *Rochelia*, as well as *Lepidium*, are certainly adhesive, and it is probable that most of the other plants have also more or less adhesive fruits or seeds.

On the mounds made by the Suslik (*Citellus pygmaeus*) he found, besides some of those on the marmot's mounds :—*Kochia prostrata*, *Sisymbrium sophia*, *Artemisia achilleaefolium* and *Echinospermum patulum*, *Ceratocarpus arenarius* (a *Chenopodiaceous* plant of which the fruit is armed with 2 very sharp spreading spines), and *Ceratocephalus orthoceras* (*Ranunculaceae*), a low herb with long produced styles to the achene.

Small mammals seem to have a fondness for disembarrassing themselves or their companions from burrs attached to their fur. A fox-terrier I once possessed was very fond of pulling off from my trousers all the spikelets of *Chrysopogon aciculatus* which had attached themselves during a walk in Singapore Botanic Gardens. He only did this when we returned to the bungalow, and then pulled out every one with his incisors and threw them on the floor. These spikelets did not adhere to his hair as they did to my clothes.

Adhesion to Clothes.—The dispersal of herbaceous and shrubby plants by adhesion to clothes of man has doubtlessly been going on ever since human beings invented cloth, and has played a very considerable part in the dissemination of the smaller plants and especially of the grasses. Everyone knows how, after a long country walk over fields and heaths, their trousers become covered with adhesive fruits of all kinds, and the same occurs wherever natives go who wear long clothes reaching below the knees. Many of these fruits are brushed off by bushes at some distance from where they were picked up, the others are detached by the wearer at camps, resting places or villages, and often form a large proportion of the vegetation surrounding a village, or on the edges of a road or track, and account for the very wide distribution of many species. In addition to the adhesion to clothes, many plants are dispersed by becoming attached to bags and sacks, and are so conveyed from one country to another across the sea. This must be taken into account when dealing with the floras of oceanic islands visited by ships, even at irregular or quite casual times.

Woodruffe-Peacock, in " A Fox Covert Study," and in a list sent to

Miss Brenchley, of seeds attached to clothes, and given in her "Weeds of Farmland," supplies a suggestive account of what he has found so carried about in England. They are fruits of *Geranium Robertianum*, *Ranunculus arvensis*, *R. bulbosus*, *R. acre*, *Geum urbanum*, *Circaea lutetiana*, *Myosotis arvensis*, *Heracleum sphondylium*, *Medicago denticulata*, *Galium aparine*, *Taraxacum dens-leonis*, *Rumex sanguinea*, *Triticum repens*, *Dactylis glomerata*, *Alopecurus pratensis*, *Bromus sterilis* and *B. racemosus*, *Festuca elatior*, *Arrhenatherum avenaceum*, *Hordeum murinum*, *Trisetum flavescens*, *Holcus*, and seeds of *Listera ovata*.

The number of grasses is noticeable, and many more might be added, since these plants in many cases have a very wide and rapid distribution, and it may also be noted that while most of these fruits are specially adapted for adhesion originally to the hair of animals, others, like the *Geranium*, *Taraxacun*, *Heracleum* and *Listera*, possess other means of dispersal, and are *adventitiously* dispersed by adhesion, for they are mainly dispersed by wind.

As Kerner states, the tufts of hairs which clothe some fruits and seeds and act as parachutes or wings, often get entangled in the hair and feathers of animals, and thus effect their dissemination.

"The rough coats of the sheep, oxen, goats and horses are always found "to have such hairy fruits and seeds attached to them after they have "passed through ground on which herbaceous composites, shrubby "willows, etc., grow at the season when those plants are in fruit. I have "removed from the coats of animals of the above kinds, fruits and seeds of "*Anemone sylvestris* (those of *A. nemorosa* are mentioned by Woodruffe-Peacock "as adhering to clothes) and of various species of the genera *Calamagrostis*, "*Crepis*, *Cynanchum*, *Epilobium*, *Eriophorum*, *Lactuca*, *Lagoecia*, *Micropus*, *Sonchus*, "*Senecio*, *Populus*, *Salix* and *Typha*."

This adhesion of the normally wind-dispersed plants to hair of animals or cloth is especially common when the vegetation is wet with rain or dew, as anyone who walks through wet grass in summer can testify. The plume-hairs seem to attach themselves readily when wet. *Taraxacum* fruits, though provided with short spines on the body of the fruit, cling to cloth more readily by the plume. Some of the plumes of Composites, e.g., *Senecio vulgaris*, are actually mucilaginous when wet. Fruits merely rough with hairs, such as those of the Thrift (*Armeria*) and the glumes of *Holcus*, readily attach themselves to cloth and can be so dispersed, but such fruits rarely remain attached for any very long period, so that they are seldom conveyed to any great distance. It is the specially armed adhesive fruits which are most successful in utilising animals and birds as transport agents.

I will mention some other cases of dissemination by these means which are of some interest.

The bracken (*Pteris aquilina*) is, like most ferns, largely distributed by wind, its light spores being readily carried about, and it is very widely distributed over continental areas, though curiously absent from oceanic islands. It is abundant in sandy soil especially, in the Malay Peninsula in open places, but absent entirely from the wet shady forests. In the plateau of the mountain of Gunong Tahan, though a suitable spot for its growth, when first visited by Mr. Robinson in 1906, it was entirely absent. This mountain is quite surrounded by dense forest, and, owing to difficulties of access, had never been visited by man, not even by the wild tribes. I visited the mountain in 1910, and beneath the raised floor of Mr. Robinson's old house, and also beneath one occupied by a surveyor a year or two later (1908), I found 2 or 3 plants of the bracken. No more were to be seen over the whole plateau, which is of great size. It is usual, in camping here, to put the rice sacks and other such baggage beneath the raised floor (or *lantei*, as it is called) of the hut, to protect them from rain, and there could be little doubt that the spores

of the bracken had been brought in the baggage-sacks to these spots, probably from the low country, many miles away, as the men passed through it with their loads.

In the greater number of cases in which we have special modifications for adhesion to animals, the mechanism appears to be originally developed in order to attach the seed or fruit to the ground where it can germinate successfully. This is noticeable in the viscid seeds of *Plantago*, and again in the fruits of *Pumilio* (*Compositae*) as shown by Darwin. Here the seeds and fruits do not exude their mucilage till they are wetted, so that they may be drifted along the dry or sandy soil till they come to a wet spot, where the exudation will cause them to adhere. This mucilage, however, will also cause them to be attached to a passing animal or bird, so that they may be widely scattered. Again, the spirally twisted awns of the fruits of *Erodium* or of the glume of *Stipa* primarily are adapted to cause the fruits to bore into the ground when wetted, and the stiff hairs at the base also play a part in preventing the fruit from being withdrawn from the soil during the boring action of the awn, but the same mechanism causes the fruits to bore into the wet and greasy fleece of the sheep, the hide of the ox, or the mouth of a horse. The hooked bristles on the seed of *Barclaya* are the evolution, or one might say the exaggeration, of the papillae, so common on the seeds of herbs which are dispersed by rain-wash, and which serve as anchors to attach them to the soil in suitable spots for their germination and growth. The same principle applies to the teeth of the perianth of *Rumex*, the acute awn-like sepals of the *Amarantaceae*, the hooked prickles of the capsule of *Triumfetta* and many other fruits.

In *Uncinia* an abortive branch of the panicle forms the adhesive organ, a case of arrested development, as is the case in the abortive flowers of *Achyranthera*. Both of these seem to be modified for animal dispersal only, and in *Geum*, *Erodium*, and *Streptogyne* persistence of an accrescently developed style plays an important part. The style of *Geum*, however, was originally plumed, so that the fruit was dispersed by wind before it was modified into an adhesive organ, as has been already pointed out (*see* p. 142).

It is interesting to know that the greatest evolution of adhesive fruits and seeds, at least by hooks and prickles, has taken place in open sandy spots, not in deserts nor in forests, since herbivorous animals do not abound in these districts as they do in open, low grassy regions. Adhesive-armed fruits are most abundant in the Mediterranean region, from Spain and Morocco to Greece, the Balkans, through South-West Asia to Persia. Except for the flocks and herds of man's domestic animals, there are but few herbivorous mammals in this area now; but from Eocene to Pleistocene days the whole of this area was covered with herds of ungulates, which doubtless brought about the evolution of these burr plants, which of later years have been widely distributed by clothed man, his goats, sheep and cattle, to far distant regions.

PORTIONS OF PLANTS ADHESIVE TO ANIMALS.

It occasionally happens that portions of plants, viscid, scabrid, or hairy, become attached to animals, in some cases carrying mature seeds, sometimes being of such a nature that, when detached, they can grow and form new plants. Thus Mr. S. T. Dunn had in Hongkong a small woolly-haired terrier dog which, rambling about in the bushes in search of rats or other game, constantly returned bearing a collection of adhesive fruits in its hair. On one occasion it came back home with the leafy culm of a *Carex*, with fruits attached, adhering to its tail. The species proved new to science, and was called *Carex canina* in honour of its first collector. The plant has no hooks or

spines, but the leaves have scabrid or minutely-toothed edges by which, doubtless, it adhered to the dog's tail. In the same way sheep carry about fragments of *Galium aparine*, and probably also grasses with attached fruits.

Cerastium glutinosum and *C. tetrandrum* are annuals living in dry spots, banks, and rocks. They are both covered with viscid hairs, gland-tipped, and when the seeds are ripe, the whole plant is readily attached to a passing animal and is so borne off, the seeds being shed as it walks along.

W. Beebe (in "Galapagos Islands," p. 315) writes of *Mentzelia aspera* (*Loasaceae*):—"The ground was covered everywhere with a dense growth "of *Mentzelia aspera*. The hairs, which covered stems, twigs and foliage, were "recurved and gummy, so that they stuck tightly. If one sat down on a "section of the springy mattress-like growth, the entire foliage came away "upon one's clothing, and in walking through this vegetable quicksand my "skin and garments became plastered with the leaves. This was the foundation "of many hundreds of nests of frigate birds and red-footed boobies." I cannot see that the hairs in this plant are hooked; they seem to me merely short and straight, but undoubtedly viscid. The bush is common in South America, and no doubt was carried to the Galapagos Islands by sea-birds, as fruits and all are sticky, and, doubtless, fragments with fruit and seeds were at some time conveyed to the island.

Mentzelia multiflora (*Nuttallia multiflora*), of Western North America, is also said to cling to clothing tenaciously; the leaves and stems are covered with short viscous processes. The Indians rub the legs of a boy with the plant when he first mounts a horse, apparently that he may adhere to the animal.

R. W. Peacock (*Agric. Gaz., N.S. Wales*, 1904, p. 628) says that *Echium violaceum*, introduced into Australia, is thus dispersed by sheep, fragments of the plant as well as separate seeds being borne about adhering to the animals.

Maiden (*Agric. Gaz. N.S. Wales*, 1916, p. 236) says that in Australia *Opuntia aurantiaca*, an introduced Cactus, breaks into small joints, and is transported long distances with facility by adhesion by its spines to the hocks of animals. Johnston confirms this (Report of Prickly Pear Commission) saying mules and cattle carry joints attached to their limbs. Marloth says the same of it in South Africa, and that the joints are dispersed also by adhesion to transport wagons, and also by rain-floods and streams, so that it has become a nasty weed.

The same method of transport is also found in the desert regions of North America and Mexico, where the *Cactaceae* are indigenous.

Toumey (in the "Vegetable Dissemination of Opuntias") writes of *Opuntia Bigelowii*:—"It is not an unusual sight to see cattle with scores of "the young joints of this (cactus) attached to their heads and legs. They "may be carried for miles, and, after weeks of travel, will grow." Berthoud, in his account of the seeds, etc., carried across country in the hair of bisons, also specially mentions hairy twigs of *Euphorbias* and fronds of *Cactus* as transported in this way (*see* p. 536).

Massart, in his travels in the Algerian deserts, found that *Forskahlea tenacissima* (*Urticaceae*) was largely carried about by mammals. He says that the branches readily disarticulate, and as they are armed with stiff hooked hairs, they fix themselves on the hair of animals. The fragments root when they fall on the ground, and the plant continues to grow. It is a very hairy sticky shrublet, the fruits of which are enclosed in cup-like hairy bracts. It is found in the deserts of Algeria, Egypt, Aden and Scinde. There are a few other species of the genus inhabiting the same area. One, *F. viridis*, is found in Arabia and Socotra, *F. angustifolia* in the Canaries, and *F. procridifolia* in the Cape Verde Islands. All grow in rocky or sandy spots, and may perhaps have reached the island by adhesions to birds, but there is reason to suppose

that Aden, Socotra, and the Canaries and Cape Verdes were formerly attached by land to the mainland of Africa, in which case they might have been in early days transported by wandering mammals.

Pemphis acidula (*Lythraceae*).—This plant is usually dispersed by sea, but it appears also to be occasionally disseminated by the attachment of the seed vessels, attached by the broken peduncle, to sea-birds. Guppy says that in North Keeling or Cocos Island the frigate birds and boobies make their nests of twigs of this shrub. These birds have often been observed to be greatly incommoded by the number of seed vessels entangled by broken stalks in their plumage, and he says: "I have been informed by residents that some- "times the bird has been killed by this cause." I have myself frequently seen boobies nesting in the branches of this bush in Christmas Island.

Adhesion by Branchlets of the Inflorescence.

The widely-spread genus of grasses known as *Setaria* (*Choetochloa*) possess dense or rather lax, often spike-like panicles of small spikelets surrounded by involucels or whorls of barren branchlets in the form of stiff bristles which are armed with spreading or reflexed barbs. By these bristles the whole head of spikelets is often attached to clothing, or animal's fur, and torn off and borne away, the small round grains falling off as the bearer progresses. *S. verticillata* is a very widely-distributed grass, occurring in Africa, India and South America, which migrates extensively in this way. C. E. Hubbard (in "East African Pasture Plants") says it adheres much to stock in Africa, and Grant (in "Speke's and Grant's Travels") records also the adherence of its heads to clothing. In Fernando de Noronha we found it very troublesome, the heads strongly adhering to our clothes by its armed bristles as we walked along.

S. viridis, *S. glauca*, *S. rubiginosa* are similarly armed, and are also of very wide dispersal, seeming largely to follow man in his wanderings, but though doubtless dispersed by adhesion, they are also carried about in cultivated grain, ballast, and other similar ways, and in some such way *S. viridis*, *S. glauca*, and *S. verticillata* from time to time appear in Britain.

The *Uncinias* (*Cyperaceae*) are an Antarctic group of Sedges, allied to the world-wide genus *Carex*, and differing in retaining an abortive continuation of the rachis protruding from the utricle, and being hooked at the tip so as to form a very suitable mechanism for dispersal by adhesion to the down of birds. The utricle of the female consists of a glume, involute and joined at the edge, containing a pistil, from the side of which is prolonged the bristle-like abortive rachis-branch, often twice as long as the utricle. The tip is bent down like a shepherd's crook, but the deflexed point presses so closely against the base as to be able to hold the finest hair (Pl. XVII, figs. 8 and 9). The fruits (according to D. Morris, in *Gardeners' Chronicle*, 1881, p. 780) attach themselves with great tenacity to the hair of dogs or the legs of pedestrians, and are removed with the greatest difficulty. On two occasions he found small birds (quits) about the size of tomtits securely caught by a couple of spikes of this sedge, which were attached to the underside of the birds with the hooked awns buried in the feathers.

The plants are found in Australia, Tasmania and New Zealand, Lord Howe's Island, Macquarie Island, Kerguelen, Amsterdam, St. Paul's and Tristan d'Acunha, Hawaii, Fuegia, Falkland Islands, Chile, Bolivia, Brazil, Mexico, Jamaica, Juan Fernandez, North America and Europe.

The European and North American species is *U. microglochin* (*Carex microglochin*), which Clarke (as it seems properly) refers to this genus. The utricle contains a small bristle, which is sometimes hooked, as in *Uncinia*. M. I. Fernald

(in Contrib. Gray Herbarium, 1926-1927, p. 61), writing of this plant in Newfoundland, says :—" Its prickly little fruits, which followed many paths, " had obviously been spread by pedestrians with their high skin-boots."

It is clear that the genus originated in the Antarctic regions, and Morris suggests that its spread northwards from Fuegia to Mexico and Jamaica is due to migrant birds on their return journey from the South of America to the North. As few or none of the Old World regular migrants go as far south as Australia, the spread of *Uncinia* is much shorter than in the New World. It is most probable that the species in the Atlantic islands were brought there by sea-birds. Mammals seem to have effected little in the diffusion of the genus, except in the case of *U. microglochin*, which may very well have been spread over the north temperate region by deer or wild cattle.

Adhesion by Armed Bracts.

Arctium, the Burdocks, spread over Europe and temperate Asia, are well known to everyone as possessing very adhesive heads of flowers enclosed in broad involucral bracts covered with stiff hooked bristles. Being tall herbs, the heads are readily attached to passing cattle, sheep, and other large animals. The achenes, which are numerous in the head, possess only a short pappus of small bristles, and in some species the achene is hairy; but the pappus is too short to float the achene through the air, and merely serves as an anchor to attach it to the ground. The burr, attached to an animal or to human clothing, permits the enclosed achenes to be dropped out gradually as the animal bearing it walks along. The plants are very abundant along paths and open country where sheep move about and human beings walk.

Xanthium (*Compositae*), the Burr-Marigolds, are herbs with the male flowers in involucres at the top of the plant, the female below (only 2 flowers), enclosed in an utricle armed thickly with hooked spines. This utricle is oblong and formed of 2 connate bracts, and from $\frac{1}{2}$ to $\frac{3}{4}$ inch long. Several species have been described, but they can be reduced to 2 or 3, of which the most common is a low erect herb with unarmed stems, *Xanthium strumarium* (Pl. XVII, figs. 4 and 5), while *X. spinosum* and *X. ambrosioides* are spiny. The first two are both natives of Europe and North America. *X. strumarium* is figured as a European plant by Dioscorides in the first century A.D., and under the name of *Lappa minor* by Brunfels (Herb., iii, 55, 1536). This establishes its claim to be indigenous to the Old World, though, with the exception of one or two species of *Ambrosia*, the remainder of the section *Ambrosiae* are American. The plant is very early recorded in England (Turner, 1551), and seems to have been much more common in those early days than it is at present. There is no doubt that it owes much of its world-wide distribution to man, being accidentally sown with wheat; and formerly in Europe and at the present day in the Indian and Malayan bazaars the fruits are sold as drugs, and used in medicine, and are often thrown upon the streets and on rubbish heaps in sweepings from drug shops. It was early recorded in England as a road-side weed. Sowerby records it as springing up from Thames mud thrown on Battersea fields. Perhaps its modern scarcity in England is due to its disuse as a drug.

Besides this dispersal by man, it is certainly spread by rivers in the flood plains. Mr. Burtt-Davy told me he had seen great abundance of the plant on the banks of the Transvaal rivers, where it had been brought by floods. But it undoubtedly owes much of its original wide distribution to transport by the attachment of its hook-armed utricles to the hair and wool of animals, and later to its adhesion to clothing of man. In the Cape and other cattle-breeding

districts it is so widely dispersed as to be a great nuisance. Mr. Burtt-Davy (in "Alien Plants of the Transvaal") says the seeds are dispersed by sheep and goats, and the tails of horses, mules, and donkeys. Mr. Perrott, of the Indian Police, sent me a number of fruits which had adhered to his trousers in a march in Peshawar District, North-West India.

One can hardly doubt that in the days when the large hairy mammals ranged across the north temperate region, it was widely disseminated by them.

X. spinosum is less abundant than *X. strumarium*, but it, too, has appeared in England in grounds where mud from the town streets had been laid down, and a plant in Kew Herbarium was raised from seed found in wheat sent from India.

X. ambrosioides is allied to this plant, but, instead of being an erect plant (as that is) it is prostrate, with smaller leaves. It is a native of temperate South America. G. Claraz, in a note on a specimen in Kew Herbarium, says:— "In the district of Bahia Blanca one meets it, especially round the burrows "of Viscachas (*Lagostoma*). I have only seen it a few years. It is prostrate and "glued, as it were, to the ground." No doubt these burrowing rodents disperse this plant by scratching the burrs off their fur at the mouth of their holes, as rabbits do the nutlets of *Cynoglossum* in England. Its native home is in Chile, but as Claraz shows, it is migrating northwards. It has hardly reached the Old World yet, but there is a specimen in the Kew Herbarium which somehow got to Geneva, possibly in South American wool.

In *Franseria* the bract enclosing the achenes resembles that of *Xanthium*, but is rather smaller and the spines are fewer, about 12 in *F. acanthocarpa*, and straight, not hooked. There are a number of species in North America, Mexico, etc., that seem to be characteristic of sea-sand and deserts, frequently occurring in islands off the coasts of Mexico and California. A few go as far south as Bolivia, Peru, and Chile. One of the most common species, *F. tenuifolia*, has been found as a roadside weed in Hawaii, no doubt introduced accidentally by human agency from America. The hooked spines on the utricle of *Xanthium* are evidently more effective than the straight ones of *Franseria*.

Acanthospermum (*Compositae*).—In this small genus of weedy plants the achene is included in a bract which is armed with hooked spines, much as in *Xanthium*. The fruits, however, are much smaller. *A. hispidum* has a triangular fruit densely covered with hooked spines and with 2 long straight spines at the top. This plant appears to be a native of tropical Africa, whence it has spread to Southern India, where, it is said, it is becoming very common, and it occurs also in Honduras and Florida, where it has appeared on ballast heaps. In *A. australe* the head of fruits consists of 4 or 5 radiating from the centre and being quite covered with short hooked spines, but with no terminal ones. The fruits are ¼ inch long. *A. hispidum* is abundant in South America, including Fernando de Noronha, but has been transported to North America (where, as it occurs on railroads, it was probably carried in ballast), the Transvaal, Singapore, where it occurs in roads through villages and towns, first being collected in 1861, and in Hawaii. It does not seem to be found anywhere else, and it is quite obscure as to how it got to Singapore, as there is no direct connection with South America.

An interesting plant is *Dicliptera Maclearii*, of Christmas Island, where it is endemic. It is one of the *Acanthaceae*, a weedy plant 2 or 3 feet tall. The flowers have 2 sets of bracts, the outer one needle-like, ¼ inch long, the inner one orbicular, stalked, ending in a sharp needle-like point. When ripe, the whole of the fruit with the broad spiny bracts breaks off and attaches itself strongly to cloth, and no doubt also to the feathers of birds, so that the enclosed seed is easily carried about. The genus is widespread, though not common, all over Africa and tropical Asia. In most of the other species the bracts are orbicular, or ovate and acute, but the mid-rib is not carried beyond the flat part of the bract.

In *D. Maclearii* the mid-rib projects a considerable distance beyond, forming the needle-like point. A similar structure occurs, however, in *D. leonotis*, of the Philippine Islands and Wetter Island, a rather remote islet, where, like *D. Maclearii* in Christmas Isle, it has doubtless been brought by birds.

Blepharis boerhaaviaefolia (*Acanthaceae*).—This herb, widely spread over Africa and the dry parts of India and Ceylon, varies from a low prostrate herb to a slender plant about 1 foot tall, with numerous axillary flowers surrounded with 4 papery bracts armed thickly with spreading recurved spines on the edges, with numerous short hooks. The whole head of bracts, over ¼ inch long with the fruit, breaks off and adheres very strongly to clothing and fur of animals, and is so transported. Mr. Burtt brought a mass of these heads, 2 or 3 inches long, which attached themselves to his clothing in Tanganyika Territory, Africa. The wide distribution of this plant is undoubtedly due to its transport in this way.

Pteranthus echinatus (*Illecebraceae*).—A little prostrate plant with axillary flowers. Here the peduncle is obovate, thick and flat; at the top of it are a number of pedicels forming a tuft with small spiny recurved bracts, each bearing a small flower with a single-seeded fruit. The whole is detached below the peduncle, and the hooked bracts serve to attach it to a passing animal (Pl. XVII, fig. 6). This is a native of the Algerian desert, Egypt, Arabia, Mesopotamia, Persia and Palestine, and has been found in Malta.

Some of the small *Urticaceae* have bracts armed with hooked bristles; among these are the fruits of *Helxine Soleirolii* of Corsica, a creeping matted plant commonly grown in gardens as a rock plant. The utricles are surrounded by a 3-winged involucre armed with hooked hairs on the edges. These might easily be dispersed by mice or such small animals running over the plant.

Rousselia lappacea, of the West Indies, has also an involucre of 2 round bracts dotted over with hooked spines.

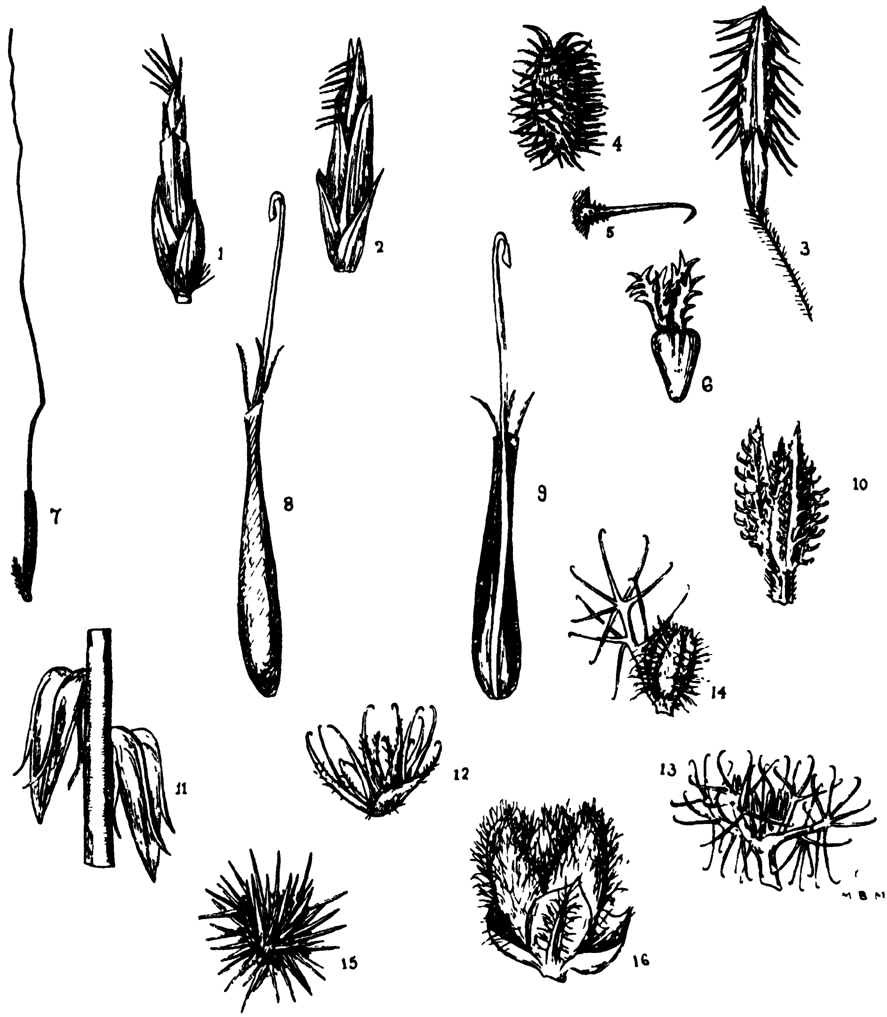
Adhesion by Glumes of Grasses.

The stiff-awned or spiked glumes of grasses are often sufficiently modified for adhesion to mammals or birds, besides which they often possess hairs or other processes which, especially when wet, readily adhere. In a walk through wet grass in the fruiting season one often finds one's trousers or stockings covered with glumes and glume-covered achenes of many grasses, not only those provided with awns, *Trisetum*, etc., but with those of unarmed grasses like *Holcus*, *Festuca*, *Poa*, etc. These plants are less often transported by birds than by mammals, as they do not adhere readily to feathers, though their presence in oceanic islands suggests that this is more frequently the case than might be expected. Though there are a certain number of grasses in oceanic islands which cannot be accounted for by adhesion to birds' feathers or sea-dispersal, still, many can be shown to have adhesive apparatus by which they may possibly be so conveyed to the island. In some cases the grasses may have been utilised in the formation of the nest, and the glumes and achenes become embedded in the plumage of the bird as it sat on it.

Huth states that *Leersia oryzoides* which inhabits banks of rivers, is dispersed by the attachment of its glumed fruit to the plumage of grebes, ducks, and moorhens, and that in this way it has been transported from South Europe to the northern German coasts. The glumes are provided with upward-pointing bristles. Woodruffe-Peacock records also the dissemination by wild-duck of *Triodia decumbens*, which has no visible adhesive apparatus on the glumes.

In oceanic islands there are seldom many grasses which can owe their

PLATE XVII.



ADHESIVE FRUITS.

FIG. 1.—*Lophatherum gracile* (spikelet, enlarged).
,, 2.—*Centotheca lappacea* (spikelet, closed).
,, 3.— ,, ,, (spikelet, open).
,, 4.—*Xanthium strumarium* (female head in armed bract).
,, 5.— ,, ,, (hook of bract).
,, 6.—*Pteranthus echinatus* (head with spiny bract).
,, 7.—*Heteropogon contortus* (spikelet).
,, 8.—*Uncinia Kingii* (utricle with hook, enlarged).
,, 9.— ,, ,, (,, ,, ,, in section, enlarged).
,, 10.—*Tragus racemosus* (spikelet, enlarged).
,, 11.—*Achyranthes aspera* (heads, enlarged).
,, 12.—*Cyathula prostrata* (head and bract, enlarged).
,, 13.—*Pupalia orbiculata* (cluster of flowers, enlarged).
,, 14.— ,, ,, (single flower).
,, 15.—*Sclerocephalus arabicus* (head, enlarged).
,, 16.—*Aerua floribunda* (flowers with bracts, enlarged).

[*To face p.* 560.

presence there to the adhesion of their glumes to wandering birds. In Christmas Island was *Ischaemum nativitatis*, an endemic species related to some of the Polynesian Islands only, of which the spikelets, which broke off very readily, were hairy and awned. In the island it was clearly dispersed by the wind, but it could not, in the first instance, have reached this spot in this way, and it was doubtless brought attached to the plumage of some bird. A small species of *Digitaria*, *D. virens*, also endemic there, had the glumes edged with short stiff bristles. It was allied to a Javanese species inhabiting sandy plains, in which the edges of the glumes were fringed with silky long hairs, which would serve to aid in wind-dispersal.

In Fernando de Noronha were a number of common grasses, probably introduced attached to clothes or baggage by the inhabitants, but one species, *Gymnopogon rupestre*, was endemic. It possessed glumes with long scabrid awns, and no doubt was introduced by adhesion to birds. *Oplismenus compositus* appeared very early in Christmas Island, and in Krakatau by 1919. This grass seems to get about everywhere very readily. It is probable that it reaches the islands by the aid of birds.

Spartina arundinacea, the Antarctic Tussock Grass, is abundant in South Georgia, Amsterdam, St. Paul's Island, Tristan d'Acunha and Gough Island. The glumes of the spikelet are armed with short, sharp, upward-pointing spines on the edges, which might readily be attached to the breast plumage of one of the sea-birds which sit or nest in the tussocks. It is possible that its rhizome may be sea-dispersed, as I have mentioned (*see* p. 331), but it is perhaps more likely that it has been carried from one island to another by sea-fowls, the spikelets being embedded in their down.

Several jungle grasses possess adhesive apparatus for attachment to passing animals. In the dense forests, where there is no wind to disperse the fruits of the grasses, and no open rain-wash to bear the seeds away, the only chance of a grass being disseminated is by wandering animals. It is true one sometimes finds grassy tracks through the forests, made usually by man, and covered with small species of *Isachne*, and on high mountains, where the forest is more open, one may find the tall *Isachne albens*, but in the thick dark forest itself one only comes across a few broad-leaved species, all of which have some kind of apparatus for attachment to the fur of animals. One of these is *Lophatherum gracile*, a broad-leaved grass about 2 or 3 feet tall, with a spreading panicle of green spikelets ¼ inch long. The spikelets have 3 lower glumes, of which the third is shortly awned, and contains the flower. Above this the rachilla is prolonged, and bears 8 or 9 abortive glumes reduced to awns, which project in a tuft at the top, and, when dry, become hooked, and, besides, are armed with minute decurved processes, by which they attach themselves to a passing animal's fur or to the cloth of a travelling native, and, breaking off from the spike, are borne away (Pl. XVII, fig. 1). The plant is common along tracks of man or wild beast through the forest. It is found in China, Japan, Formosa, India, Ceylon, Tonkin, the Malay Peninsula, Java, Sumatra, Borneo, Labuan, the Philippines and New Guinea. Another species in China is quite unprovided with any apparatus for attachment to wild beasts. I would suggest that this grass originated in China or the Eastern Himalaya, and has been carried by wild beasts, certainly in the Malay Peninsula mainly by wild pigs, and by attachment to clothes, southwards to the eastern islands.

Centotheca lappacea, an allied grass, has a different mechanism. The spikelets are much smaller, about ⅛ inch long. They are borne in a panicle on slender branches with upward-pointing hairs, and on the fourth glume, which contains the seed, are on each side a row of deflexed white spines from tubercled bases, very stiff. As these point away from the tip of the pendent spikelet, they catch very readily in cloth or fur, and the whole spikelet, and sometimes the whole

panicle, comes away from the plant. So readily and strongly do these spikelets adhere to cloth, that the Malays call it "Rumput Silat Kain" (cloth-spoiling grass).

It is very widely distributed, being found in India, Ceylon, China, Formosa, Andaman Islands, Siam, the Malay Peninsula, Java, Borneo, Banca, Sumatra, Labuan, Celebes, Philippines, New Guinea, North Australia, nearly all the Polynesian islands except Hawaii, West Tropical Africa and Madagascar.

There are two other species referred to this genus from Africa, which are unarmed, and do not inhabit forests. They seem to be rather local and not widely spread.

The wide continental distribution of this plant is easily accounted for by wild beasts and men travelling through the forests, but its presence in so large a number of the islands, unless caused by accidental conveyance by man, suggests that the plant is sometimes conveyed by birds. However, it was absent from Christmas Island and from Krakatau as late as 1919.

Tragus racemosus is a short grass with an erect culm bearing a terminal spike of small spikelets ⅛ inch long, of which Glumes II and III are thickly coriaceous, and armed on the backs and ribs with long hook-tipped spines, which are readily adhesive to the fur of animals (Pl. XVII, fig. 10). It inhabits sandy places and dry pastures in South Europe, Asia Minor, Afghanistan, South India, China, Africa, Canaries, Socotra, St. Helena (1865), Australia (1874), North America, Texas (1847), West Indies, Brazil (1829).

It seems probable that this grass is disseminated by cattle or sheep. Miss Hayward found it at Tweedside, evidently brought in sheep's wool. Allied to this are three other monotypic genera, *Latipes* and *Dignathia* of sandy open country in Africa, and the curious *Lopholepis*, of which the spikelets resemble the minute head of a bird, of South India and Ceylon, all of which have the 2 stiff glumes armed with tubercles ending in hooked spines or stiff hairs. These three are less widely distributed than *Tragus*, doubtless because the latter, which grows further north in a cooler region, comes more readily into contact with the sheep and cattle of the Mediterranean region and Asia Minor, hence its appearance in St. Helena, Australia, and America.

Chrysopogon aciculatus, Love Grass.—This grass has a creeping stem, short leaves, and a tall slender culm about 6 or 8 inches tall, bearing a short dense panicle of small spikelets about ¼ inch long. These spikelets break off very readily, with short peduncles attached to them armed with stiff upward-pointing short yellowish bristles, by which they adhere strongly to cloth and the fur of animals. The peduncle penetrates actually into the cloth and remains firmly attached. In walking on turf composed of this grass, the trousers get covered with these little spikelets, hence the plant is called Love Grass. It grows in open dry turfs in great abundance where it occurs. It is found in China, India, Ceylon, the Malay Peninsula, Java, Sumatra, Borneo, Amboina, Philippines, Australia (before 1867, not common), Cook Island, Polynesia (most islands), St. Helena (1865), Mauritius and Seychelles. I believe it was originally a native of India, and has been carried attached to clothing or animals' fur to the remaining localities.

Echinolaena scabra is a South American grass in which the outer glumes of the spikelets (which are lanceolate and arranged on one side of a rachis close together) are covered over with stiff bristles from dilated bases. It is doubtless transported by adhesion to cloth or fur, but I have no record of its natural history. It is found in Guiana and Brazil.

Pseudechinolaena polystachya, an allied plant, is a slender broad-leaved grass with a lax panicle of spikelets ⅛ inch in length. One glume (Glume II) is armed with hooked bristles by which the spikelet is readily attached to clothes and fur of passing animals. It grows on the edges of forest paths

in tropical Africa, India, Ceylon, the Malay Peninsula, Java, Sumatra, Tonkin, and in America from Mexico to Paraguay. The distribution of this plant is interesting, for it is one of the few jungle plants common to both hemispheres. As it is obviously not dispersed by birds, it is clear that it is one of the plants which shows a former land connection between South America and Africa. It shows little or no signs of association with man, as do many adhesive fruited plants, and is undoubtedly transported almost exclusively by terrestrial wild beasts.

Eriochloa ramosa.—An open-country grass in which the glumes are softly hairy. The rachis of the panicle is usually scabrid, but the spikelets break off from the rachis and take no part of it with them. It is recorded as being found at Tweedside, evidently brought in sheep's wool, and this may account to some extent for its very wide dispersal, but I have not noticed that its spikelets are adhesive. It usually occurs by roads and paths, and by river banks, and is found in Astrakan (1835), tropical Africa, India, China, Siam, Malay Peninsula, Java, Philippines, St. Helena (1808), Australia (1804), Ascension, West Indies, Guiana. It appeared in Krakatau before 1919. I here include *E. acrostichum*, which is hardly specifically distinct. A rather distinct-looking species, *E. subulifera*, occurs in Aldabra. There are a number of species in South America. It is a good fodder grass, and in some cases may have been introduced in this way, but this would hardly account for its presence in the islands.

Cenchrus.—A genus of grasses usually found in deserts or sand by the seashore, of which many species have been described, and which could probably be reduced to a few, occurring in all warm parts of the world. The spikelets have an involucel of hard acute spines, sometimes at the base, often scabrid, and enclosed is a spikelet, sometimes hairy, with 1 grain. These spikelets are arranged in a spike, from which, when ripe, they readily break off. As I have twice found the plant on the seashores of small islands, I have little doubt but that the spikelets are to some extent sea-borne. *C. viridis* is found in the Malay Islands, Siam, South America, Fernando de Noronha, West Indies, and seems to me to be closely allied to *C. catharticus* of India and Africa, of which Capt. W. P. B. Beal writes on a specimen at Kew :—" This " grass is a nuisance to Europeans, as its fruit sticks to trousers and socks, " and scratches."

C. calyculata seems to be most abundant in the Polynesian Islands, New Caledonia, Pitcairn, Kermadec, Fiji, and Sandwich Islands. *C. echinata*, with rather larger spikelets, is found in tropical Africa and the Mascarene Islands, Easter Island, Fiji, Hawaii, Kermadec, South America, West Indies and Bermuda.

Gossweiler, in Kew Herbarium, writes of it in Africa : " The goats are " sometimes covered with the fruits of this grass."

As goats were very early carried about and distributed in various islands by early explorers, it is most probable that these burr-spikelets were carried about on them, and this will account for their distribution in many places.

Themeda arguens is a low grass, from 6-18 inches tall, with large spikelets in which the grain is about $\frac{1}{3}$ inch long, cylindric, with an acute base covered with stiff yellowish-brown erect hairs, shortest at the base, but longer towards the tip, and ending in an awn 3 inches long and shortly roughly hairy. These fruits adhere readily to clothes, and are probably carried about in this way. It is a native of the Malay Islands, and occurs in Singapore and Penang and in Australia (1802–1805), and also in the Andaman Islands and Annam. It has been introduced into Jamaica as a fodder plant, and seems to have spread there.

Heteropogon contortus.—This grass is a well-known pest to sheep, horses, and cattle. It is from 1 to 3 feet tall, with a solitary erect spike. The Glume IV

is reduced to an awn 3 to 5 inches long, spirally twisted at the base, scabrid, and coming away from the grain, which is about ¼ inch long; at the acute base is a tuft of upward-pointing hairs, very stiff (Pl. XVII, fig. 7). The spiral portion of the awn untwists, when damped, in an extraordinary manner, and in so doing drives the sharp point, armed with its hairs, into the wool or hair of an animal, and eventually may penetrate the skin. Hackel states that it bores into the wool of sheep, and may penetrate to the intestines, where it proves fatal. Pancher says: "Nuit beaucoup à moutons et un peu au gros "betail," in New Caledonia. Major Appleton says it causes much trouble to ponies, the spears sticking in their mouths, in Somaliland. All kinds of horses and cattle seem to be fond of the grass when young, but when the fruit is ripe, will not touch it. This spear grass occurs in Italy, Tyrol, and other parts of Southern Europe, Canaries, Tunis, Cape Verde Islands, Morocco, Socotra, Africa, Mauritius, India, Malay Peninsula (not common), Siam, Java, Sumatra, Timor, Philippines, Australia (1802-1805), Polynesia, North and South America, and West Indies.

There is no doubt that it has been carried to most of these places in the fleeces of sheep or hides of cattle. In the Malay Peninsula it is uncommon, partly, perhaps, because sandy spots suitable for its growth are not very plentiful, but largely because sheep are not brought there. The few places where I have seen it were usually near towns or villages, where it might have been brought by cattle, horses, or goats. It is absent from islands and other spots where domestic animals do not go. I found it once at Pekan, in Pahang, but, as there are no animals on that sandy area which could transport it, it had not spread at all. *H. triticeus*, with even larger awns, a native of India, has been met with in Java and Australia (1802–1805), no doubt similarly introduced.

Aristida ascensionis.—A low dry-region grass with a dense spike-like panicle of spikelets in which the grain is enclosed in a glume terminated by a long slender tripartite awn, ¾ inch long, by which it can be readily attached to the fleece of sheep or to the hair of goats. The callus at the base of the spikelet, which is detached with it, is barbed in many species of the genus, and penetrates into the fleece or hide of an animal, and Hitchcock says of *A. fasciculata*, in North America, that the 3 awns spread widely, and are caught by the wind, which carries the spikelet with the barbed callus forward, and this catches in the fur of an animal. Webb, who collected specimens of *A. ascensionis* in the Cape Verde Isles, says of it: "A very brittle grass, the "broken stems and awns form little balls that stick on the legs, and are an intolerable nuisance." The distribution of the genus seems, indeed, to be due to the adhesion of the spikelets by the awns or the barbed callus to the skins of animals, and as there are 2 or 3 species in the Galapagos allied to South American kinds, doubtless to birds also, though, as they are largely absent from oceanic islands, this perhaps does not often happen. That they are not rarely carried about by sheep nowadays is shown by the occurrence of *A. angustata*, a native of South Africa, as a wool-borne alien in Tweedside, and the statement of Hackel (in the "True Grasses") that the seeds of *A. hygrometrica*, of Australia, bore into the wool of sheep and penetrate to the intestine, where they prove fatal. *A. ascensionis* was probably originally a native of North Africa, and brought early to the north coast of the Mediterranean. It was first collected by Sir Hans Sloane in Madeira, on his way to Jamaica in 1688. It was described as a Madras plant by Plukenet in 1696, and was found in Ascension Island by Cunningham in 1698. The first person to visit the Island of Ascension was Joao de Nova Castella, in 1501. He visited St. Helena in 1502, and landed a number of goats, asses, and hogs there, and it is very probable that he also carried some of these animals to Ascension Island, and in their hair brought

the *Aristida*. However, it is noticeable that of the few other plants collected and recorded by Cunningham on Ascension (only 3 in number), none were plants likely to be introduced by man, and this grass does not occur in St. Helena.

Besides the localities already mentioned, the grass is found in the Canaries, North, East and South Africa, Arabia, Aden, all over the dry parts of India, the north of the Malay Peninsula, China, the Mascarene Islands, Brazil and Peru. It is a grass of dry sandy and rocky warm places, and its absence from the wet tropical regions is only to be expected, but wherever the country is suitable and goats or sheep have travelled, this plant seems to have accompanied them.

Stipa.—A large genus of grasses with much the same adaptation for boring into the hair, fleeces, and hides of animals as those of *Aristida*, *Heteropogon*, etc. The calli are often bristly, so that they would naturally retain a better hold on the skin, and the awns often plumed, the action of the wind on which would also assist the boring action. The various species have the worst reputation for boring into the skins of animals. They inhabit dry, sandy or rocky spots, and are more abundant in Europe, Asia and America than *Aristida*, but less common in tropical Africa. There are as many as 40 species in Australia. *S. tortilis* is common in the Mediterranean region, Egypt, Asia Minor, North India, Canaries, Madeira, and Africa. An endemic species occurs in Easter Island, *S. horridula*. It is difficult to account for this unless its ancestor was introduced by some bird. *S. bicolor* is found in Juan Fernandez (1824), but as it is an American plant, and cattle had long before that been introduced to that island, it probably was an accidental human introduction. Otherwise the genus seems to be quite absent from oceanic islands, as well as from places like the Malay Peninsula, where sheep are not brought.

Hackel records *S. capillata* and *S. spartea* as boring into sheep, and 9 species from South America have appeared in the wool-waste in the Tweedside, including *S. Neesiana*, which has been found in similar places in France, Italy, and Germany, and a few years ago a fine clump of it appeared on the Mortlake rubbish dump in Surrey. The fruit of this species has also a bad reputation in the Argentine for boring into the skins of animals and inflicting serious wounds. *S. Lessingiana* is, as I have already mentioned, dispersed by marmots in Siberia.

Chloris barbata.—A tall slender grass with a plume-like purple tuft of racemes of small spikelets, each containing a grain. The outer glume is hairy on the edge, and as these fine hairs seem to attract small particles, it is possible that they are viscid. A long awn projects from the glume, and this, like the awn on the smaller inner glume, is armed with short up-pointing teeth. By these awns the spikelet, which is readily detached from the rachis, is attached to cloth or fur.

The spikelets are light and liable also to be blown away from the plume by the wind, and are to some extent dispersed in this way. The plant appears to be a native of India (Rheede, 1769), but is now rather widely dispersed, mainly from its spikelets adhering to sacking or merchandise, as it is largely a wharf plant. It thus occurs in Hongkong, Macao, on the Pescadores, Batavia, Singapore, Johor, Bangkok, Manila, Mahé (1852), Mauritius (1854), also in Brazil (1829), San Domingo (1827), and the Cape (1818). In most of these places, e.g., Batavia, Singapore, and Johor, where I have seen it, it is very abundant along the wharfs, but has spread no further, as there is no suitable sandy country for it to spread to. Some of the other species, such as *Ch. scariosa*, have been found in wool at Solothurn, Switzerland, "in lanis exoticis" (Probst), and *Ch. Gayana*, of tropical Africa, has been introduced into Australia and Hawaii, and as a fodder plant into Jamaica.

Oplismenus.—A very widely-distributed shade-loving grass of warm countries, with a slender lax terminal spike of distant or close-set spikelets. The two lowest glumes are awned, and the third has a shorter process; the outer glumes are often hairy. The spikelets fall off whole very readily. A number of species have been described, but most seem to be forms of two. *O. Burmanni*, native of India, occurs also in Siam, Malay Peninsula and islands, Africa, Cape Verde Isles, Socotra, Madeira, Brazil, and the West Indies. In the Malay Peninsula at least, it is only found in or near towns, and is clearly carried about by man or animals. *O. compositus* is bigger and much more common, especially if we include the closely-allied *O. undulatifolius* and *O. hirtellus*. The form or species known as *undulatifolius* is found in Europe to India, and China and Japan. An ornamental cultivated variety has been widely spread in gardens, and perhaps accounts for its appearance in such localities as the Philippines. Typical *O. compositus* is found in China and Japan, Bonin, Liukiu and Formosa Islands, India, Nicobars, Andamans, Siam, Java, Sumatra, Christmas Island (1897), Borneo, Celebes, Papua, Australia (1819), Kermadec ("probably introduced," Macgillivray), New Zealand (1852), Polynesia to Hawaii, tropical Africa, Seychelles (in vanilla plantations), Madagascar, North and South America and West Indies. It appeared in Krakatau in 1919; there had been before this a settler for a short time in Krakatau, and Ross had made a settlement in the bay of Christmas Island in 1888, and certainly had accidentally introduced some weeds; but though this grass is now the most common in the island, I did not see it in 1890, although Andrews found it in 1897, before any animal but a goat had been introduced. It is quite clear that it is a very easily-dispersed plant, as is shown by the number of islands it has reached, but unless it is carried by human clothes or baggage or by attachment to animals, it is difficult to see how it gets about. As it is a good fodder grass, it is possibly carried in fodder for herbivorous animals, but this reason will not apply to Krakatau nor Christmas Island.

Echinaria capitata, a dwarf grass from 2 to 8 inches tall, with a solitary, dense head of long, projecting, spined glumes with sharp scabrid tips, occurs along the Mediterranean on both sides, and as far as Mesopotamia.

Aegilops ovata.—A desert plant with a short spike of few spikelets, the outer glume ribbed and scabrid or hairy, with 4 stiff scabrid awns, the inner glumes with 2 awns each. The whole spike is about 1 inch long, with the awns as long, and breaks off entire at the base. This is a native of South Europe, Morocco, Palestine and the Canaries. I have also seen a single plant from Pernambuco. Massart mentions an *Aegilops* as adhering to his rug in the Algerian desert, perhaps this species, but there are several allied ones in this area.

Bromus unioloides.—Of this plant, the fruits adhere to wool (according to Huth), and other species of *Bromus* have already been recorded by Woodruffe-Peacock as adhering to clothes.

Trisetum, *Holcus*, *Alopecurus*, *Festuca elatior*, and many other grasses are commonly attached to clothing by their awns, if they have them, or the sharp-pointed glumes, or simply by the rough hairs on the glumes. In *Holcus mollis* I find that the short projecting spines on the back of the glumes are quite sufficient to make it adhere strongly to cloth.

Triodia (*Sieglingia*) *decumbens*.—A short grass with a sub-racemose panicle of few spikelets, with no awns, and not very hairy. It frequents heaths and moors. Woodruffe-Peacock (*Journ. Bot.*, 1916, p. 359) writes:—" My brother " Max told me that the wild-duck are very fond of seeds of this grass, and in " July and August frequent spots on the peaty heath for them. At this time " they are moulting and can fly with difficulty. If a duck be shot dead on the " ground while feeding on the *Sieglingia*, more or less of the seed may be " found on its back. It is undoubtedly spread in limestone heaths by this

"means, and by the circular storms and whirlwinds at the same time of the "year."

ADHESIVE PERIANTH-LOBES.

In the weedy *Amarantaceae*, *Cyathula* and *Pupalia* the flowers are in small heads on a long slender terminal spike. Of these there are only one or two perfect ones in each cluster, the rest being barren and reduced to stiff bristles hooked at the tip. When ripe, the whole cluster, brushed by clothing or a furred animal passing by, breaks off and attaches itself by the hooked abortive flowers. In this way the very common village weed *Cyathula prostrata* has been carried far and wide over Africa, Madagascar, India and Malaya to Polynesia, Cook's Island, New Zealand and Brazil. Though probably carried to some of the islands by adhering to the plumage of birds, it owes its extreme abundance mainly to its attachment to human clothing (Pl. XVII, fig. 12).

In the allied genus *Achyranthes* the flowers are stiffly reflexed against the rachis of the long slender inflorescence, the stiff bracts have a long acute point, and the bracteoles are also spiny, while when the fruit, a small nut, is ripe, the petals also become rigid and spiny, so that the whole inflorescence, terminal and long projecting, catches readily in clothing, fur or feathers, and the fruit, with the perianth, bracts, and bracteoles all detached together, adhere to the passers-by, whether man, beast, or bird (Pl. XVII, fig. 11). The most common species, *A. aspera*, is found in the Canaries, Algiers, Sicily, Madeira, Cape Verde Islands, India, Malaya, Australia, Polynesia, Christmas Island (before the first visit of man), Cocos-Keeling, Mascarene Isles, Chagos, Comoro, Aldabra, South America and the West Indies. This very abundant plant is certainly to some extent distributed by human aid. It sticks to the clothes and is very annoying, as Macgillivray says of it in the Isle of Pines, but its occurrence in so many little-visited and hardly-inhabited islands, and especially in its presence in Christmas Island, where it was collected by Lister in the first expedition to that island, and in Cocos-Keeling Island, where it was collected by Darwin in 1836, proves that it is not seldom carried about by birds.

Chenolea (*Bassia*) (*Chenopodiaceae*).—Salt bushes found in the deserts, steppes, and saline swamps in Egypt, temperate Asia, and Australia. In some species the plants have the habit and fruits of *Suaeda fruticosa*, but in many the fruits are plumed, with long hairs, or are woolly and wind-dispersed over the flats, while others have the fruits armed with 5 sharp spines at the top. These spines are the hardened lobes of the perianth which encloses the achene. They could readily be dispersed by their adherence to the feet of birds walking on the mud flats, as in *Tribulus*, *Triumfetta*, etc.

This genus affords another example of closely-allied species possessing modifications for wind-dispersal and adhesion dispersal respectively, so characteristic of desert and steppe herbs and shrublets.

Sclerocephalus arabicus (*Illecebraceae*), a small prostrate plant occurring in the deserts of Algeria to the Persian Gulf and Nubia, and Cape Verde Islands, and has occurred in the Canaries, but perhaps here accidentally introduced in ballast or in some such way. The flowers are in small heads of from 4 to 7, the perianth-tube encloses the utricle, containing a 1-seeded ovary, and is adnate to the bracts, the 5 lobes of the perianth become spiny, so that in fruit the whole head forms a spiny ball, the spines are slightly curved, and the ball is very adhesive to cloth or fur. Massart describes how, in the Algerian desert, these little adhesive balls, blown into camp, adhered to his rugs (Pl. XVII, fig. 15).

Adhesive Calyces.

Among the herbaceous *Verbenaceae* are some that possess adhesive calyces. One is the tall slender herb *Phryma leptostachya*, with a long slender raceme of distant flowers. When the corolla has fallen, the small tubular calyx is sharply deflexed. Three of the sepaline points are much longer than the other two, and sharply hooked at the tip. The deflexed calyces suggest a resemblance to those of *Achyranthera*. The plant inhabits woodlands, as so many of these adhesive-fruited plants do, and is found in India, China, and North America, especially the western part. It is certainly distributed by adhesion to mammals wandering through the woods, in which case the distribution strongly suggests the former existence of a land connection between Northern Asia and North America, by which the animals could have transported the seeds.

Priva is a genus of similar habit, with the calyx quite round, about ⅛ inch through, covered with short hooked hairs. *P. bahiensis*, of Brazil, has also nucules armed at the back with a keel of numerous strongly-recurved hooks. *P. hispidus* and *P. echinata* have similar calyces, and are found in Mexico, South America, and the West Indies, and I have seen specimens from New Caledonia. *P. leptostachya*, a very similar plant, occurs in tropical Africa and India. These plants, like *Phryma*, are almost certainly dispersed by the attachment of the fruit to the fur of wandering mammals, though I do not find any observations made on this point. The allied genus *Verbena*, chiefly South American herbs, mostly possess hairy calyces which certainly at times may become attached to animals' hair or wool, and fruits of *Verbena spuria* are known to have been found in sheep's wool. The English Vervain (*V. officinalis*), so abundant on the edges of paths, is adhesive from its glandular viscid hairs to passing animals, and is fully described under the account of adhesion of fruits by viscid exudation (p. 612).

Spilanthes acmella, the Tooth-ache plant (*Compositae*).—This small herb is now widely distributed all over the warm parts of the world. The genus is represented by a number of species, including *S. acmella* in South America. It is a plant of from 12 to 16 inches tall, with small heads of yellow tubular flowers, which are very pungent to taste, and hence are used to apply to the gums in toothache. Several species in South America possess yellow ray florets, and *S. grandiflora*, which occurs in the Philippines, and *S. ovata* (probably the same plant), in Australia, have also these ray florets. They are both allied to *S. acmella*, and may be original forms of it. A very distinct species, *S. anactina*, occurs in Australia, Borneo, and Labuan. Otherwise *S. acmella* is the only species, and far the most common in the Old World. It is generally found in waste ground, near villages and along road-sides. Though usually a rather fugacious annual, there are perennial creeping forms, and even a shrubby one in Africa, where it is very common. Another form, var. *oleracea*, has very large heads, about ½ inch long. This seems almost always to occur in or about gardens, and seems to me a cultivated form only. The achenes are very small and black, with 2 erect spines on the top, and a number of stiff hairs pointing upward to the top on each edge of the flattened achene. It is by these that it adheres to cloth and animals' fur and is carried about, though it is also aided in its travels by its utilisation in medicine. Where there are no dentists, the natives suffering with toothache can only obtain relief from the use of irritants to the gums, and the flower-heads of this little weed supply his requirements, hence they are carried about dried by medicine-men and others, and their small achenes, easily detached, are dropped by village or road.

Originating from Brazil, where it appears to grow wild in open heath-like country and in damp spots, it has migrated to the West Indies, China, Formosa, India, Ceylon, Siam, the Malay Peninsula, Java, Sumatra, Borneo, New

Caledonia, all over tropical Africa, where it is very common, and the Mascarene Islands. I found it in Christmas Island in 1890, doubtless introduced by Ross's people, who had settled there some time before, but it disappeared again, and was not seen before or after that time. It is absent from Polynesia, Fernando de Noronha, Krakatau (to 1919), and most islands.

Synedrella nodiflora (*Compositae*), a yellow-flowered weed, native of South America and the West Indies, has a small head of flowers sunk in rather large broad bracts. The ligulate flowers have a flattened oblong achene, with the 2 edges serrate and the 2 sepals broad and toothed on the outer edge. The achenes of the central tubular flowers are narrower, and not serrate-edged, the sepals are slender and toothed.

This plant does not seem to have reached the Old World very early. It occurs in South India (1899), Assam and Ceylon, Andamans (1867), Siam, Penang (1886), and many parts of the Malay Peninsula, Java, Borneo, Philippines, Amboina, Christmas Island (1897), Hongkong, Samoa (1904), west coast of Africa (1900), Krakatau (1919). It is obscure as to how it originally reached the Old World, but it has since been dispersed by its adhesive achenes, and also, I believe, with cultivated plants. In some of the localities given above it is sporadic and quite casual, but in suitable cultivated ground it grows very plentifully. In Christmas Island, where it was accidentally introduced from Singapore, probably in pots of cultivated plants, or perhaps in packing, it grew too abundantly near the Settlement, for, being an annual, it dried up in the dry period and took fire very readily. Its slow spread—compared with *Ageratum*—is probably due to its involucral bracts not spreading, as in that species, but enclosing the achenes and preventing their being dispersed by wind or ready attachment to passers-by. The plant reached Krakatau by 1919, but a European with coolies settled on the north-eastern side of the island in 1917, and they may have brought it, or it may have been accidentally brought, attached to baggage, by one of the earlier expeditions.

Ageratum conyzoides Linn. (*Compositae*).—The *Ageratums* are strictly confined to South America, except for this one species, the White-Weed of planters. It is an annual plant, from 1 to 2 feet tall, with small heads of pale blue or white flowers. The achene is long, 5-angled, black, with short acute thorns on the edges. The pappus consists of 5 scales, broad and spiny at the base, ending in long points armed with short spines. They do not appear to be at all viscid, but attach themselves to animals' hair or human clothing by the spines on the achene and pappus scales.

This plant was undoubtedly originally a native of South America, but it has now spread over all warm countries. It is wide-spread over the whole of Africa, and occurs in Egypt, Cape Verde Islands, Madeira, India, China, Japan, Malay Peninsula and Archipelago, Kermadec group, New Hebrides, Tonga, Samoa, and, of course, South America and the West Indies. It was very common on the main island of Fernando de Noronha, but not on the smaller islands, and was found in Christmas Island by Andrews in cultivated ground in the Settlement in 1897, before the introduction of cattle or ponies to the island, though later, as the ponies largely fed on it, it was conveyed to the tracks in the island. It had not reached Krakatau by 1919, which seems to suggest that it travels far more by its adhesion to clothes or hair than by wind, as its very widely-dispersed companion, *Vernonia cinerea*, which is altogether dispersed by wind, arrived there early. It is strictly a weed of cultivated ground, and though largely distributed by its spiny fruits, it seems likely that wind plays a small part in its dispersal locally, for it is not adapted at all for long-distance flight. I have found it far in the interior of the Malay forests at Telom, in a clearing made by the wild tribes, and it is possible that the achenes are

transported by attachment to roots of tapioca or other plants cultivated by them, and carried about to plant from place to place.

Verbesina alata, of Jamaica and other West Indian Islands, has broad flat achenes with a wide corky margin and 2 powerful hooked spines. The whole round fruit-head, 1 inch across, is thickly armed with these stiff hooks. It has, however, not as wide a distribution as the *Ageratum*.

Bidens (*Compositae*).—This genus now extends nearly all over the world, but mostly in temperate tropical areas. Few species occur in the Old World, but in America the genus is very varied and finely developed, and as all its allies, e.g., *Cosmos*, are of South American origin, there is little doubt that it was in this area that the genus developed. At the same time it is certain that one species, *B. tripartita*, still common in Britain, was abundant in Europe in Pliocene days, and, if the genus originated in America, must have reached Europe or temperate Asia in very early days. The plants are annual herbs, 1 foot or more tall, with the usual structure of a composite, and possessing heads of tubular and sometimes ligulate flowers as well. The achenes are armed with decurved hooks on the body and on the 2 to 4 sepaline spines representing the sepals. They are very adhesive to clothing and fur of animals, and to the plumage of birds.

Bidens cernua is common in Europe except in the extreme north.

B. tripartita, with 2 (rarely 3) hooked sepaline spines, is more common, and is spread over Europe, temperate Asia to Japan, China and India. The fruits of both of these species are buoyant, and can be readily dispersed by streams. *B. chinensis*, which closely resembles the latter, and has yellow ligulate flowers, is found in India, Borneo, Aru Islands, the Philippines, Timor Laut, Australia, Africa, Cape Verde Islands, and Bourbon.

B. pilosa is more of a warm-country plant. Unlike *B. cernua*, it is an inhabitant of dry spots in forests and open country. and does not frequent marshes or river banks. There are two forms, one with white ligulate flowers and one without, but both are found together in the forests. It occurs in Egypt, Mesopotamia, Canary Islands, Madeira, Azores, all tropical Africa, where it seems to be very common, Madagascar, India, China, Malay Peninsula, Borneo, Philippines, most of the Polynesian Islands, Kermadec Isle, New Zealand, Bermudas, Florida, and all over tropical America. This plant appears to owe more to human transport, by the attachment of its armed achenes to clothing, than to its dispersal by animals or birds. In Bermudas, Azores, Florida, New Zealand, and probably the Malay Peninsula, it seems to have travelled by the adhesion of the fruits to cloth or packages, though perhaps, in some cases, sheep's fleeces. I have gathered it far in the interior of the Malay forests, but chiefly in or near the abandoned camps of the wandering wild tribes. It is quite absent from oceanic islands, and had not reached Krakatau by 1919. There are several (5) kinds of *Bidens* in Hawaii, all related to South American species. These were probably descendants of plants brought from the mainland by birds.

Glossogyne has achenes resembling those of *Bidens*. The 2 sharp spines of the achene are often barbed, as in *G. pinnatifida* of India. *G. tenuifolia* has a wide distribution from Siam, Philippines, Australia, New Caledonia, Fiji, Isle of Pines, China and Formosa. A similar structure is found in *Heterosperma* and *Cosmos*, and several other allied genera. *Cosmos*, which has 2 or 5 spines on the achene, is now widely distributed from America (its home of origin) over the Old World, from its cultivation partly as an ornamental plant and partly as a potherb by natives.

Blainvillea rhomboidea.—A small coarse weed with the achenes usually rough, and with 3 needle-like sepaline points at the tip. It often occurs in waste cultivated ground, but, as it is especially abundant in open country in Brazil,

is probably of South American origin. It is common in the Old World in Africa, Arabia, Cape Verde Isles, Socotra, Madagascar (a note, without date, in Kew Herbarium says " newly introduced "), St. Helena (1868), Baluchistan, India, Ceylon, Yunnan, Malaya, Australia (1808), South America, West Indies, Fernando de Noronha, and Galapagos. Stewart (in the " Flora of Galapagos ") writes : " The fact that this plant occurs on such a remote island as Abingdon " would show it was not a recent introduction." Indeed, in such a case, transport by birds is suggested, but it must be remembered that these islands were very early visited by buccaneers and whalers from South America, and as it is probable that much of this plant's distribution is due to its armed achenes adhering to sacking, baggage, and such things, it is possible that it was introduced by some such method by these people.

Among the *Compositae* we find some species with plumed fruits in which the body of the achene is provided with hooks or short processes, which serve to anchor the flying fruit to the soil or in a crevice of rock or wall with which it comes into contact. Among these are the Dandelion (*Taraxacum dens-leonis*) and Sow-thistle (*Sonchus*). It is quite common to find dandelions growing in cracks of walls in which the achenes have been retained by their hooks. The achenes of both *Taraxacum* and *Sonchus oleraceus* and *S. asper* are known to attach themselves to clothing, partly at least by these hooks, though they are also retained sometimes by the pappus, especially when wet. This was probably the cause of the appearance of *Sonchus oleraceus* at White Island, near New Zealand (*see under* Sepaline Plumes, p. 147), and in a number of other islands to which the fruit could not have been transported by wind.

We have, however, some very curious instances of *Compositae* in which the achene was originally plumed and so wind-dispersed, but the plumes have disappeared, or become functionless, and these body hooks so exaggerated that the achene is entirely adapted for dispersal by adhesion to the fur of animals. The most striking case is that of *Rhagadiolus* (*Hedypnois*), of the Europeo-Asiatic deserts. In R. *papposus* the plume is well developed, and in R. *pendulus* the plant is large and the achenes only slightly thorny. In R. *hamosus* the pappus seems to be present in the young fruits, and disappears as they ripen. In these spiny-fruited species the achene is strongly curved, and the spines are greatly developed on the outer curve edge, and usually the pappus has more or less completely disappeared on the outer achenes in the head, while it remains persistent on the inner ones, which appear to be sterile.

We have here clearly a transformation of plumed, wind-dispersed fruits into plumeless, thorny, adhesive ones. As the plume becomes more aborted and ineffective, the body of the achene becomes more fully armed with hooked processes. This reaches its maximum in *Koelpinia*, a low, tufted plant with spreading stems which end, in fruit, in a circle of very remarkable crescent-shaped achenes about 1 inch long, very strongly armed on the outer curve with hooked bristles (Pl. XVIII, figs. 3, 4). At the top are some hair-like processes which may be the remains of a pappus. These plants, *Rhagadiolus*, *Koelpinia*, etc., are all natives of the Mediterranean region, from Spain to Persia, Morocco, Madeira and the Canaries. The most widely distributed is R. *cretica*, which, covering the Mediterranean region and the islands, has also appeared in Texas, Uruguay, and Australia, undoubtedly introduced in the wool of sheep or hair of cattle. It seems difficult to account for the transformation of a wind-dispersed plant occurring in open sandy plains to one dispersed by adhesion to animals, as one would have thought the former design would have been the one more certain and effective.

The evolution of the adhesive fruits of *Ageratum conyzoides* and such world-wide distributed plants is intelligible, as in their case the only fruits which could be dispersed so widely across oceans would be the adhesive ones ;

but this cannot be the case in plants confined to a desert or steppe area, where animals (exclusive of domestic ones) appear to be comparatively scarce.

All the species of *Rhagadiolus* do not have these extraordinary hooked or spine-armed achenes, though nearly all are more or less adapted for dispersal by attachment to animals' hair. *Rh. stellulatus* has quite smooth achenes, but they are drawn out into long points and hooked at the tip, and, when ripe, spread in a star-shaped manner, so that they would readily catch in the hair of a passing animal by the terminal hooks (Pl. XVIII, fig. 8).

Another Composite with strongly-armed large achenes is *Dipterocomè koelpinioides*, a native of Persia and Afghanistan (Pl. XVIII, fig. 5). It belongs to the section *Calendulaceae*. *Calendula*, the Garden Marigold, has large incurved achenes with short processes on the back, and no pappus. They do not appear to be at all adhesive, the processes being too short to adhere to cloth or short fur. *Dipterocome*, a dwarf plant, has large achenes resembling those of *Koelpinia*, but curved outwards, not inwards, so that the two ends nearly meet. The back is armed with numerous strong forked spines furnished with many hooks. These curious fruits are about 1 inch long (Pl. XVIII, fig. 5). In another genus, *Acanthocephalus* (*Harpachne*), small herbs growing in Altai and Afghanistan, the back of the curved achenes is also armed with stiff strong hooks, but they do not spread, the whole head of fruit forming a prickly ball (Pl. XVIII, figs. 1 and 2).

A rather curious story is that of the South American weed *Eleutheranthera ruderalis*, which appeared in Krakatau in 1919. This plant was only known, in the Old World, at that time in the Buitenzorg Botanic Gardens and their environs, and the puzzle was as to how it arrived at the island. As the previous expedition had started from the Buitenzorg Gardens, I came to the conclusion that its achenes had been brought accidentally in the baggage, and the plant had established itself. Mr. Burkill has pointed out that I collected the plant in waste ground in the Gardens of Singapore some years before, and shows that, while some of the achenes are smooth, others are armed with short tubercles. It is with these, doubtless, that it adheres to the cloth or baggage. How it got over to the East is obscure, but it has only arrived lately, and is spreading slowly.

Aster tripolium, the Sea-Aster, a well-known tidal and sea-rock plant of England, is dispersed by wind with the aid of its plumed pappus, and also by the floating of its seeds and seedlings, as is elsewhere detailed, but it is to some extent probably disseminated by birds.

E. Kay Robinson (in *Countryside*, September 30th, 1905, quoted by Guppy in the "Naturalist in the Pacific," 605) says that snow-buntings eat the seed on the English coast, and suggests that the draggled fluff, still carrying the seed, might adhere to the bird. As the hairs of the pappus are furnished with short processes, this may well be; but the achene itself is provided with short stiff bristles, so that the fruits might certainly adhere to the down of the bird, especially if wetted. I have already called attention to the possibility of adhesion of Dandelion and Sow-Thistle achenes, and it is quite possible that this method of distribution may be more common than we think. There was published in a police magazine a curious case of a murderer being partly convicted from the discovery of the achene of a scarce composite attached to his clothing and borne about by him for some days, the plant itself being found near the site of the crime.

The herbs of the order *Boragineae* are very largely dispersed by adhesion to animals.

Myosotis, the Forget-me-nots, are widely-distributed herbs, often with hairy and adhesive tubular calyces, which become readily detached by an animal brushing past the racemes, and, adhering to its fur, carry with them the very

small nutlets which lie at the bottom of the tube. I here speak of the typical species of the northern hemisphere, for there are a large number of very dissimilar forms referred to this genus in New Zealand and elsewhere, which I exclude from these remarks. The Water Forget-me-nots, *Myosotis palustris*, *M. coespitosa* and *M. repens*, also are not dispersed by mammals, for, growing as they do in very wet spots where animals do not go constantly, such adaptations would be of no use. In these the hairs on the calyx are appressed and soft, and useless for dispersal. *M. palustris* is mainly dispersed by floating portions of the stem, as the nucules do not float of themselves. It is common in Europe, temperate Asia and North America, and Madeira, and a plant was recently found in Ceara, Brazil, 50 miles inland, where it may have been brought by some horticulturist.

The English downland plants, *M. arvensis*, *M. collina*, and *M. versicolor*, are widely dispersed by small mammals, especially rabbits. On the Wiltshire Downs I find the plants close to rabbit burrows, and on spots where these animals sit to sun themselves and clean their fur. The calyx-tubes at the base are provided with hooked hairs, while the hairs at the tips of the sepals are usually straight. The calyces readily attach themselves to the fur of animals or human clothing, and break off from the pedicel, and the nucules fall out when the animal scratches itself (Pl. XVIII, fig. 11). The loose soil at the mouth of the burrows, where the rabbits dig, form suitable spots for the growth of the plant. I had abundance of *M. arvensis* var. in my garden at Kew, and my dog, running about among it, came in with its long hair full of the calyces, and abundance of the polished black nucules were also entangled in it. These downland species have appeared casually in the Azores and North America; *M. arvensis* in rubbish heaps in Prince Edward's Island and a few other spots, as has *M. versicolor*; *M. collina* in New Zealand, Motu Ilu Island (1872), probably introduced in sheep's wool. *M. australis* of Australia (1836) and New Zealand (1850) seem to be allied to *M. versicolor*, but the hairs on the calyx are rather spiny, and the fine *M. suaveolens* of Australia (1804), seems to be allied to it. Is it possible that these are evolutions of one of the European species?

M. sylvatica is a woodland plant with the calyx-tube armed with hooked hairs. It is abundant in Europe and Asia Minor, in the Cameroons and along the mountain ridges to South Africa, and also occurs in North America. The New Zealand species are utterly unlike this set of European species, as are the two indigenous ones of the Azores.

Next to *Myosotis* we have a small genus *Rochelia*, of which a few species range from North Africa and Asia Minor to Persia and Northern India. These are mostly dwarf plants resembling Forget-me-nots, but possessing narrow linear sepals, strongly hairy and connivent at the tips over the one or two nucules, which are papillose and enclosed in the sepals as in a cage. In R. *cardiosepala* the sepals are broad and triangular, meeting by the edges with gibbous processes at the base, and quite concealing the nucules. It occurs in Persia and the Western Himalayas, where Duthie says it is found on sheep-grounds, and doubtless all the species are dispersed by these animals. R. *stellata* is recorded by Formosov as occurring on the hillocks thrown up by marmots in Siberia (Pl. XVIII, fig. 9).

V. M. Spalding (in "Distribution and Movements of Desert Plants") writes:—"At certain seasons of the year it is impossible to walk about "on Tumamoc Hill, Arizona, without carrying on one's clothing a collection "of burrs of *Harpagonella*, the siliques of *Thelypodium lasiophyllum* or the equally "tenacious fruits of other genera." (The latter plant, a Crucifer, does not appear to me to have any method of adhesion, as the siliques are quite smooth. Possibly they are mucilaginous when wet.)

Harpagonella is a local, almost prostrate little plant (confined to Arizona

and Guadeloupe Island. The 5 sepals, which are long in proportion to the fruit, are stiff and covered with short sharp hooks. It is easy to see how readily they may be carried by passing animals.

Marrubium vulgare (*Labiatae*), the Horehound, is a native of Britain, and in a wild state is to be found on dry downs, often chalk, but, being a popular drug, it occurs in many places where it has escaped from the herb garden. Generally a low, woolly herb, it possesses in its calyx a ready means of dispersal. The calyx-tube is about ¼ inch long, woolly, and furnished at the mouth with 10 ascending and spreading hooked spinous teeth, containing at the base 4 obovate oblong small nucules or 1-seeded carpels. By the hooks round the mouth of the calyx it is readily attached to fur, and as the calyx is easily broken off from the head of flowers, it can be carried away with the nucules by a passing animal, such as a rabbit, the nucules eventually falling out of the tube. I have several times seen this plant at the mouth of rabbit burrows, where it has doubtless been carried by these animals, and the seeds shaken out of the calyx when the rabbit scratches off the burrs which have adhered to it in its rambles (Pl. XVIII, fig. 14).

The White Horehound is found all over Europe, Persia, Morocco, Syria, Afghanistan and North India, Balearic Isles, Madeira (Desertas Island), Canaries and Azores. It seems rare in these islands, and perhaps has been introduced by man. It is also met with, undoubtedly as an escape from cultivation, in California (1833), Mexico, Argentine, the Andes of Chile (1825), and Buenos Ayres (1820), and New Zealand (1866). There are a number of other species known in the Mediterranean and temperate Asiatic regions, but except *M. echinatum*, of the Atlas Mountains, which has much longer hooked bristles at the calyx mouth, in none are the calyx lobes hooked though often spiny. It is probable that these spiny calyx-lobes do attach the calyx to animals, but they cannot be as effective as the hooks of *M. vulgare*. *M. alysson*, of Algeria, has 5 triangular lobes spread out in a star form, and these are very likely to attach themselves. It is said to grow on the edges of fields. *M. deserti* is an interesting species, as it grows in the deserts of Tunis and Algiers, where there are, according to Massart, no animals to carry its fruits about, wherefore the sepals are very short, ovate, and blunt, and are useless for adhesive dispersal purposes.

A large number of the other *Labiatæ* have the 5 sepal points drawn out into stiff pungent needles, and frequently have hairs on the tube, which, combined, may serve to attach the calyx with its nucules to fur or plumage; and to be effective in this way it is essential that the calyx must be readily detached when the nucules are ripe, which is not the case in such labiates as *Lamium*, in which the sepaline points are flaccid and not spiny. In such plants the nucules simply fall out and are dispersed by rainfall, or by the aid of ants.

Another remarkable Labiate in which the sepals are prolonged into hooked spines is *Nothochaete hamosa*, of the Himalayas and Yunnan. It is a tall rough herb with the flowers in whorls like those of a Dead-Nettle (*Lamium*), but larger. The whorls are 1½ inch across; the 5 calyx-lobes are developed into stiff spines ½ inch long or more, each terminated by a sharp hook. The tube is wholly hairy. When the fruit is ripe, the calyx-tube is readily detached from the whorl, and is easily carried off by a passing animal brushing against it, and carrying in it the nutlets, much as in the case of the horehound (*Marrubium*). It is probably dispersed by sheep or other large animals.

In most *Labiatae* of this type the calyx is not detachable from the stem when the fruit is ripe, but remains firmly attached to the plant. In these plants, however, in which the sepaline points are hooked, the tube containing the nutlets is very easily detached. The importance of this minute difference is, of course, very great in the matter of dispersal. Unless the calyx broke off

as the animal brushed against it, the clinging hooks would be useless. It is by these two factors combined that these plants are adapted for dispersal by mammals.

It is probable that the Labiates with spine-pointed calyces which we find in oceanic islands owe their presence there to attachment of their spines to birds, and probably the larger sea-fowl. In Christmas Island there grew plants of *Leucas javanica*, a herb widely distributed in the eastern islands, Java, Celebes, Timor Laut, Little Kei, Philippines, Tonga, Fiji, and Samoa and Hawaii, Australia (Malden Isles) and Coral Isles (collected by Beechey). I am here including the plants known as *L. flaccida* and *L. decemdentata*, which are at least closely allied, if not mere forms. It is just possible that the plant, first found in Christmas Island in 1890, was brought there accidentally by the Ross family, as it was not found by Lister, though this will hardly account for its general insular distribution.

In Christmas Island there is also a tall widely-distributed Asiatic herb, *Anisomeles ovata*, in which the calyx ends in 5 sharp points, and is all hairy with rough hairs. I find in the Christmas Island form that these sepaline points are prolonged into stiff bristle-like hooked points and covered with short processes, so that they might be attached to the plumage of birds. I have seen a similar form at Lake Toba, in Sumatra. The plant was found in the island by Lister, before any human beings had settled there, so that the only way to account for its presence is by adhesion to some bird. A species with similar calyx, *A. salvifolia*, a native of Australia, is also an insular species occurring in Little Kei, Trinity Island, and other islands off the Australian coast.

In Krakatau the swamp-loving *Hyptis brevipes* appeared very early in 1906. This herb is believed to be a native of South America and the West Indies, somehow introduced into the Old World. It is, however, not a weed of cultivation, but inhabits wet marshy spots. The calyx has long hairy sepaline points. It is abundant in Singapore, and has been found in the Andamans, but is absent from India, Ceylon, and apparently Java. It probably reached Krakatau by the adhesion of its calyx with nucules attached to birds, or possibly the nucules, fallen out, were picked up in mud by some wader. *H. suaveolens*, also of South American origin, occurs more abundantly in waste ground all over Asia, Africa, etc., but its mucilaginous seeds are used by natives as a drug, and it probably owes its wide dispersal to human action. It occurs in the Natuna Islands, Nicobars, and Fernando de Noronha, perhaps accidentally introduced by man. The nucules are mucilaginous when wet, and it is possible that it is due to adhesiveness of the wetted nutlets to the feet of waders that *H. brevipes* reached Krakatau.

A number of the *Urticaceae* have the achene included in the perianth, which in the female is in the form of an utricle. This is often furnished with hooked hairs, while in some the hairs are viscid. These latter are mentioned under viscid fruits (*see* p. 613).

Thus *Boehmeria cylindrica* has hooked hairs on the top of the utricle. The flowers, which are minute, are borne in clusters on a long raceme.

Pouzolzia hirta, a common weedy half-shrub or herb in China, Malay Peninsula, Java and Sumatra, the Philippines and Papua, which grows in open woods, has the mouth of the utricle provided with hooked bristles. *P. indica*, which is very abundant in damp spots in India and Ceylon and the Malay Peninsula, and also is found in China, Hainan, Formosa, Java, Sumatra, Borneo, Labuan, the Philippines, Tonkin, Sunday Island, Kermadec Group, and Australia, where it is, however, rare, has the utricle provided with numerous straight hairs, with some hooked ones. The shape of the utricle varies very much in this plant. In the common form it is flask-shaped, with 10 ridges;

in others it is 4-angled, and in the form *alienata* it has 4 wings, so that this form might be aided in its dispersal by the wind.

Urtica.—The Stinging Nettles are very widely distributed over the world, and this seems largely due to their adhesive powers to fur, feathers, and cloth. The common large Stinging Nettle (*Urtica dioica*) has axillary racemes of unisexual flowers, and both the racemes and the sepals are armed with pungent hairs. The fruit, when ripe, is a whitish flat oval achene, slightly papillose, and sometimes armed with short hairs on the edges. It is enclosed in 2 rounded inner sepals, and at the base, spreading, are 2 smaller lanceolate or oblong outer ones. All are covered with short stiff hairs (Pl. XVIII, figs. 6 and 7). When the fruit is ripe, it falls off enclosed in the 2 larger sepals, which, with the 2 smaller ones, are persistent—that is to say, they remain attached for some time after the fruit is ripe. To test their adhesive powers I walked through some clumps of nettles with ripe fruit at Kew in September, and, after walking about ½ a mile, found that 6 fruits were adhering to my clothes by the spiny hairs on the 2 pairs of sepals. Whole racemes also became attached to my clothes. Eventually, after some further drying, the achenes fall away from the perianth, but this period allows of their fruit to be borne to some considerable distance. It is very commonly associated with rabbit burrows.

Urtica dioica is common all over Europe and North Asia to China and Japan, occurring also in Mexico and tropical Africa. In some of these localities it has undoubtedly been accidentally introduced by man.

U. urens has very similar fruits and sepals, and is much more widely distributed, but the perianth seems usually much less spiny. It is found in Europe, Morocco, Abyssinia, North America, Chile and Peru and Australia (1856). It is not rare in islands, being met with in the Canaries, Falklands, and Bermuda, but in these cases mostly as a garden weed, the achenes having probably been brought in soil with pot plants, etc. In New Zealand Thompson notes that it occurs mixed with Horehound (also an adhesive-fruited plant) in and around sheep pens and camping ground.

U. pilulifera has tall branches bearing spiny globose heads of flowers with a boat-shaped hooded hairy and spiny perianth, the spines mostly outside. The achenes are large for the perianth, oval papillose, and fall with the perianth. The plant is not so widely distributed as the two previous species, and does not spread readily.

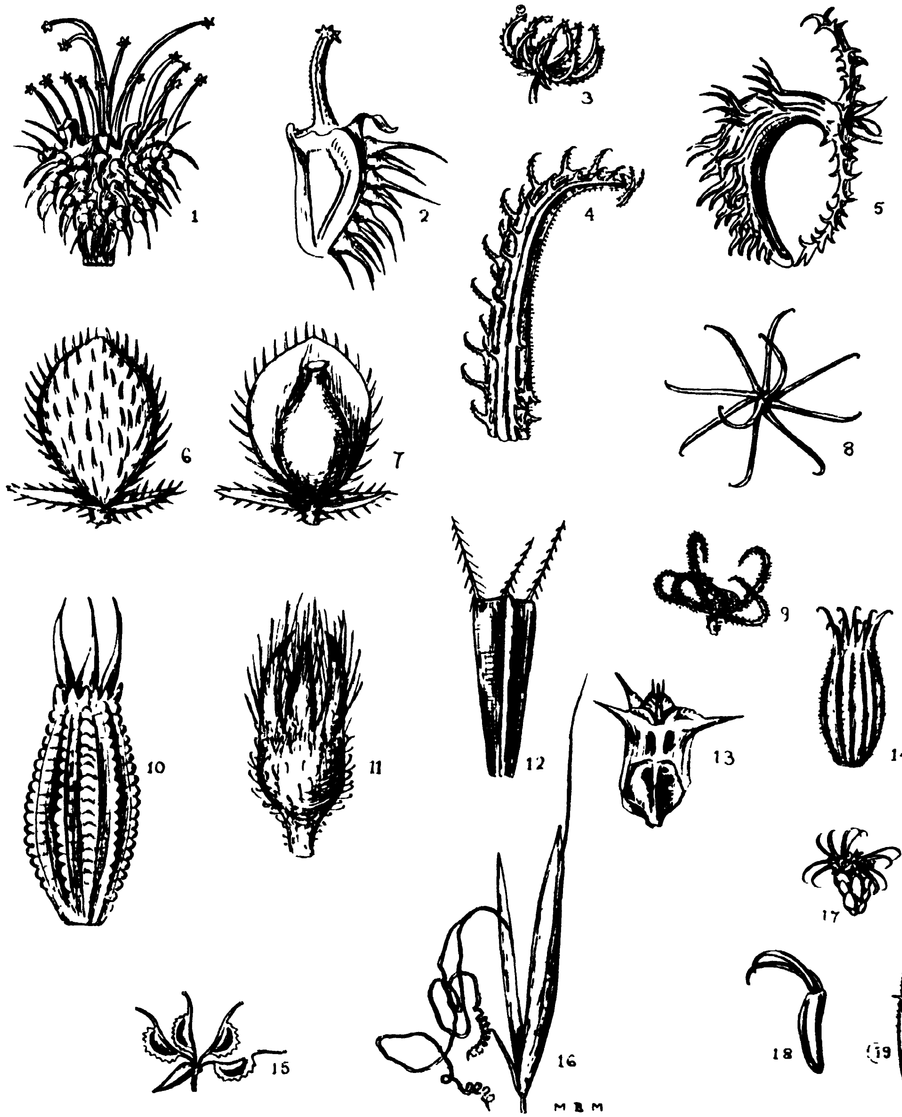
U. spathulata, of Bahia Blanca, Brazil, is recorded by G. Claraz as occurring specially round the burrows of viscachas. These animals doubtless carry about the achenes in the spiny perianth and deposit them at the mouth of their burrows, as *U. dioica* is dispersed in rabbit warrens.

U. cannabina is also mentioned by Formosov as being found on hillocks thrown up at the burrows of marmots in Siberia. The other species of the genus are widely scattered in cool temperate or subtropical regions, and it is interesting to note that many occur in islands—Canaries 4 species, Madeira 4, Azores 3, Bermudas 2 (doubtless introduced by man), Juan Fernandez and Masafuera 3, Auckland Islands 2, Chatham Island 1.

There can be no doubt that the nettles owe most of their wide dispersal over continents to adhesion of the fruits to mammals, and probably to some extent to birds also.

In many of the Docks (*Rumex*) *Polygonaceae* the persistent and accrescent sepals have spiny edges when the fruit is ripe, and by these the fruit is attached to cloth and hair and wool of animals, and probably also to feathers of birds. I have had wool sent me from New Zealand containing fruits of R. *conglomeratus*. Holmboe mentions Dock fruits as found in sheep's wool in Cyprus. Some of the fruits of these plants are very spiny on the edge; such are R. *nepalensis*, of the Himalayas.

PLATE XVIII.



ADHESIVE FRUITS.

FIG. 1.—*Acanthocephalus amplexifolius* (head, enlarged).
„ 2.— „ „ (single achene).
„ 3.—*Koelpinia linearis* (achene).
„ 4.— „ „ (single hook).
„ 5.—*Dipterocome koelpinioides*.
„ 6.—*Urtica dioica* (achene in sepals).
„ 7.— „ „ (one sepal removed).
„ 8.—*Rhagadiolus stellulatus*.
„ 9.—*Rochelia stellata*.
„ 10.—*Astrantia major* (fruit, enlarged).
„ 11.—*Myosotis arvensis* (calyx, enlarged).
„ 12.—*Bidens tripartita* (achene).
„ 13.—*Emex australis* (fruit).
„ 14.—*Marrubium vulgare* (calyx).
„ 15.—*Zannichellia pedunculata* (fruits, enlarged).
„ 16.—*Streptogyne ciliata* (spikelet).
FIGS. 17, 18, 19.—*Tragoceros zinnioides* (achenes, and head of achenes).

[*To face p.* 576.

The most spiny-fruited plant of this section, however, is *Emex spinosa*, a dock-like plant with the flowers in axillary tufts. The female flower has a 5-lobed tubular perianth; 2 of the lobes are quite small, the other 3 are larger and acute. When ripe, the achene is enclosed in the tube, and the 3 sharp lobes become acute spines. The whole fruit is about ¼ inch long, and, when fallen, lies always with one spine projecting upwards, like a calthrop (Pl. XVIII, fig. 13). The original home of the plant appears to be the Algerian desert, Egypt, Palestine, Crete and Greece to Arabia, where it occurs in sandy wastes. It is found also in Spain and Portugal, Sicily, Canaries, and South Africa, Mauritius and Australia, and has appeared as a ballast plant in Florida. Massart describes it as one of the fruits which, on awaking in the morning, he found adhering to his rug in camp in the Algerian Sahara, it having been blown in by the wind and becoming attached to the cloth. The position in which the fruit lies supported on the two lower spines allows of its being blown along by the wind over the sand, and the spines serve also as anchors to hold it if it arrives at a damp spot or crevice in a rock where it can grow. But it is also dispersed in the same way as *Tribulus* is—by attachment to the feet of animals which tread on it, the spines perforating the foot or holding it between the toes. The plant does not appear to be met with in Africa between the northern deserts and the Cape, where it is considered a serious pest, and is known as the Devil-thorn. It may have been introduced into South Africa in ballast or in sheep's wool, as it is readily attached to fleeces, or it may have disappeared owing to climatic changes between. In Natal, Mauritius, and such localities, it is chiefly recorded as a plant of the roadside, cornfield and pasture, which suggests that it is not indigenous to those localities. The history of its introduction to Australia is interesting. In 1830 the ship *Margaret*, on her way to West Australia, called at the Cape, and one of the passengers, who was going to settle in Australia, collected some fruits of the Devil-thorn as "Cape "spinach." These he took to Australia and planted in his garden. It, however, appeared to be an unwholesome vegetable, and it soon escaped from, or was thrown out of his garden, and quickly spread widely. The fruits readily became embedded in the fleeces of the sheep and also in their feet, and in those of the horses and cattle, by means of their sharp spines, and thus were disseminated everywhere. The introduction of the plant into the Sydney parks is said to be due to horses and cattle being depastured there. The plants in South Africa and Australia seem to be more robust and larger and to have bigger fruits than those of the Northern African form, which is, perhaps, due to better soil and climatic conditions.

Adhesive Corolla.

Adhesion by the persistence and stiffening of the corolla-lobes is, as might be expected, very rare, and I only know of one instance. This is a small weed of South America known as *Tragoceras zinnioides* (*Compositae*). In this plant the tubular bifid corolla persists, and becomes dry and rigid in fruit, and is strongly hooked, so that the achene might be readily attached to a passing animal and borne away (Pl. XVIII, figs. 17, 18 and 19).

Adhesion by Hooked Styles.

Ranunculus, Buttercups (*Ranunculaceae*).—This genus is spread over all the world, but chiefly in temperate regions, where the species are numerous. In the tropics it is confined to high mountains.

The Buttercups appear to have originally been evolved in the Antarctic region, where they are abundant. The New Zealand kinds possess carpels

drawn out into strong erect conical points, and very close to these are the little plants known as *Ceratocephalus*, which have the same shaped carpels, and which occur in Southern Europe, the Himalayas, and New Zealand. They were doubtless more abundant at one time, but have disappeared in the area between New Zealand and the Himalayas.

The carpels have undergone modification, apparently for dispersal purposes, into several forms. In one series the fruits are rounded and light, and the stigma has disappeared. This set is adapted for dispersal by floating, and attachment in mud to the feet of birds. Abundant in Fuegia, Chile, etc., they are represented in north temperate regions by R. *sceleratus* and by the various forms of aquatic ranunculi, *Ranunculus aquatilis*. The Antarctic species have evidently been transported in mud by birds to Kerguelen, Marion Isle, Amsterdam, Fuegia and the Falkland Islands, and Tristan d'Acunha (probably, but the specimen is doubtful, R. *biternatus*). R. *aquatilis* and R. *tripartitus* occur in Patagonia and Chile.

In Juan Fernandez is a species, R. *caprarum*, of which the fruits, rather large for the genus, have a seed not filling up the carpel, giving it the appearance of being winged. It is probably a floating-fruited species, but the stigma is distinctly hooked, so that it may have reached the island in the feathers of a bird. R. *Moseleyi*, in Kerguelen, has the style hooked likewise, and may have arrived at the island in the plumage of a bird or in mud attached to its feet.

In the next series the carpels are small, but larger than in the aquatic or mud-haunting species, and this series includes the common buttercups of our English meadows, as well as most of the tropical mountain kinds. In these the stigma is hooked, and forms an organ of attachment to fur, feathers, or clothes.

Woodruffe-Peacock mentions the adhesion of the achenes of R. *bulbosus* and R. *acris* to human clothes, and those of R. *auricomus* in mud on boots. I have found, after a walk in the pastures, the hooked carpels of R. *acris* attached to my trousers on several occasions. Miss Hayward records the occurrence of R. *trilobus* in sheep's wool, as well as two spiny-fruited species, R. *arvensis* and R. *muricatus*. R. Brown (in " Earth and its Story ") found an achene resembling that of a *Ranunculus* adhering to the feathers of a snow-bunting. The achenes of these pasture plants are also swallowed by cattle and other animals, and passed in evacuation. Achenes of R. *acris* var. have been found in the stomach of a mammoth. According to Guppy, the fruits of most of this class of *Ranunculus* soon sink in water. Those of R. *repens*, however, do not, but will float for 12 months. This plant also is often floated whole down rivers, as I have often seen in the Thames at Kew, and the plants grow readily as soon as they are drifted on shore.

In the third series the carpels are larger and armed on the sides with sharp prickles which are quite stiff when the fruit is ripe. Such are R. *arvensis*, R. *muricatus*, and R. *parviflorus*.

Most of these are plants of arable country, and are distributed in seed corn, although they are also dispersed by adherence to cattle and sheep. R. *muricatus* was found in Juan Fernandez, in Beechey's voyage in 1873. It is common in South America and Bermuda. It was also found by Burtt-Davy in ballast heaps in the Cape, and occurs in the Canaries and New Zealand. It is not seldom dispersed by adherence to sheep's wool.

R. *parviflorus* occurs in Australia and New Zealand. Woodruffe-Peacock records (in " A Fox Covert Study ") that the fruits of R. *arvensis* were attached to his clothes.

The story of the Ranunculi appears to be as I have said. The original forms started in the Antarctic region with long-beaked carpels, and from these evolved the dwarf genus *Ceratocephalus*, which is so small an annual that,

according to Kerner, the whole plant can attach itself by its spiky heads of carpels to animals, and is thus conveyed from place to place. Formosov found one species, *C. arenarius*, on the mounds thrown up by the suslik, which, doubtless, is one of the transporting mammals. Some of the Ranunculi with straight-spiked carpels found their way to South Africa, and R. *Baurii* and R. *Cooperi* much resemble the New Zealand plants in the form of their fruits. By taking on a swamp habit and a reduction of the carpel to a small size, the swamp forms, e.g., R. *biternatus*, were evolved, and, abundant in southern South America, were conveyed by birds to the Atlantic islands and northwards in America, eventually forming the Batrachium section. Other species evolved the hooked stigma, by the adhesion of which to birds and mammals they migrated north to Europe and North America and to temperate Asia, where, with other Himalayan plants, they descended south along the mountain chains to Java and Sumatra.

The Ranunculi first appear in Europe in the Upper Pliocene, the oldest species being R. *aquatilis*, R. *repens*, R. *flammula*, R. *lingua* and R. *sceleratus*. Most of these haunt wet spots, as is only to be expected, as the formations which alone have been preserved are those of swamp and marsh. The ordinary species do not appear at first sight to have as good a dispersal apparatus as many other plants, but it is clear that it has been effective in giving them a wide distribution.

Anemone.—The true Anemones have carpels like those of buttercups, terminated by a more or less hooked style. Woodruffe-Peacock states that those of *A. nemorosa* adhere to clothes.

Of *A. obtusiloba*, a native of Kansu in China, R. Farrer writes, in the "Rainbow Bridge," of "the spidery ugly tangles of this plant, that starts with "5-pointed creamy stars and ends in lanky spraying fountains, with heads "of hooky green seeds that catch to your clothes like burrs."

Erodium (*Geraniaceae*).—The Stork's Bills are low herbs, abundant in Europe and Asia Minor, and as far East as North India. The fruit consists of 5 carpels, connate at first, with long beaks surrounding a columella or receptacle. When the fruit dehisces, the separate carpels are detached from the columella. Each now consists of a single-seeded carpel, acute at the base and covered with stiff upward-pointing hairs; above, the beak is awn-like, spirally twisted at the base, and fringed with hairs on the inner face, which was previously appressed to the columella. When these carpels fall away during a dry period, the awn at the base is twisted. When it reaches wet soil or is damped by rain, it untwists, and by the pressure of the untwisted end, aided by the stiff hairs, the acute point of the carpel is driven into the ground, the stiff bristles on the base preventing it from being drawn out. When it has penetrated up to a certain point at the base of the awn, it breaks off, and the seed is thus planted. The principle is exactly the same as utilised in the grasses *Stipa*, *Aristida* and *Heteropogon*, but in those cases the grain is enclosed in a bract or glume, whereas in this case it is enclosed in its pericarp. Just as in these grasses, in some species the awn is plumed, and so the seed can be borne to some distance, and also, as in these, the seed bores often into the wool of sheep or hair of cattle, and so the plants are widely dispersed about the world.

The most widely-dispersed and abundant species is *Erodium cicutarium*, a small, usually prostrate plant with small hairy, but not plumed, awns. As in the grasses, the unplumed species are more widely distributed than the plumed ones, by attachment to animals. *E. cicutarium* is found all over Europe, Algeria, Asia Minor, Egypt, Palestine, Canaries, Madeira, India, West Siberia, China, Abyssinia, the Cape, Australia (the form with two red spots on the petals, var. *pimpinellifolium*, is recorded by Pepper as exceedingly common in Adelaide between 1840 and 1850. Gunn notes: "This *Erodium*, which had

"originally been imported to Hobart Town, has now (1847) spread about the "colony, and is common about the streets and following the roads.") It occurs also in North America (1847), and southwards through Brazil to the Falkland Islands. Ball (*Journ. Linn. Soc.*, xxi, p. 214) writes: "Widely spread from "Buenos Ayres southward through Patagonia. It is considered useful for "cattle, as it springs up afresh after each fall of rain. I have seen it in Peru "from the coast up to 3,700 metres in the Andes, and it is equally common in "Chile, and Grisebach records it from all parts of the Argentine. Like many "other introduced plants, it owes its diffusion more to animals than to the "direct agency of man."

In "Notes of a Naturalist in South America" Ball writes:—"Its extension "seems to keep pace with the spread of domestic animals, and, as far as I can "make out, it is nowhere common except in districts which are now or were "formerly pastured by cattle."

It has also appeared in the Sandwich Islands and in New Zealand (1838), and the fruits have been found in the wool of sheep at Tweedside. The seeds of this plant (and probably of other species) are also adhesive by mucilage exuded from the testa. Its so ready dispersal is probably due to both methods combined. Several other species of *Erodium* of European origin have also been carried about the world by attachment to the wool of sheep or hair of cattle. *E. moschatum*, of Europe and Asia Minor to Persia, occurs in the Nilghiris, Canaries, Madeira, Azores, Abyssinia, the Cape, Australia, New Zealand, Mexico and Brazil. *E. malacoides*, with large fruits 1 inch long, native of the Mediterranean region, has been met with in the Azores, Madeira, Canaries, Sudan, Cape Verde Islands, the Cape, on Robben Island, North India, Japan, Australia, New Zealand, Jamaica, Peru. *E. geoides*, of Patagonia (1825), may perhaps be an evolution of this plant. *E. botrys*, of the Mediterranean region, Madeira and the Canaries, has settled in Australia "all over the settled "districts," and North America. It has even been found in a sewage farm at Apperley, Yorkshire, and in wool on the Tweedside. *E. chium*, *E. romanum*, *E. laciniatum* and *E. cygnorum* an Australian species, have been found in wool-washings in Europe. The latter was found in Australia by Robert Brown, in 1802–1805; it is allied to *E. malacoides*. It is extremely difficult to see how this species can have reached Australia, for the genus is completely absent from any part of the world in the neighbourhood of that country, being, indeed, almost completely confined to the Mediterranean region, except for the species transported to other countries by flocks and herds. It does not seem at all likely that it is an evolution of so recently imported a species as *E. malacoides*.

Geum (*Rosaceae*).—A widely-distributed genus of herbs, with the flowers borne, in most cases, in lax, spreading, weak panicles, the carpels usually very numerous and hairy in a head, with long slender styles. There are two sections —one (*Sieversia*) in which the long styles are straight and plumose, with a fringe of silky hairs on each side, as in *Pulsatilla*. These are mostly Arctic or sub-Arctic, and the carpels are dispersed by wind. In the other section the carpels are usually hairy, but the hairs, except in one or two cases, do not spread up the long slender style, which is quite glabrous. The slender stiff style has a semi-loop formed in it at a distance of from $\frac{1}{2}$ to $\frac{2}{3}$ of its length from the base. The upper part breaks off from the curve of the loop, leaving a hook at the top of the persistent portion. These stiff hooks catch in the fur of a passing animal or in human clothes, and adhere very firmly. The whole head may come off in a mass, but usually the carpels attach themselves separately (Pl. X, fig. 3).

Geum urbanum is a common plant in Europe, Asia Minor, and North India, and usually grows along shady paths and open places, where it comes into contact with cats, dogs, sheep, and possibly wild animals. Closely allied to it are *G. ranunculoides*, Australia and Tasmania (1802), and *G. magellanicum*,

New Zealand (1838–1840) and Chile. *G. capense*, of South Africa, is also an ally. These plants are quite absent from the tropical regions of Africa, Asia and America, as well as from the Canaries, Madeira, and the Azores, but there are a number of species in North America, *G. macrophyllum*, *G. virginianum*, *G. vernum*, etc., as well as in China and Japan. *G. rivale* is found both in Europe and Asia, North India and North America. I should suggest that these *Geums* were evolved from the plumed *Sieversia* section in the north temperate region by the disappearance of the plumy hairs on the style, and by the formation of the kink, which, making a hook, allows them to be animal-dispersed.

The plumed *Sieversias* are Arctic, North American and European, from areas where mammals are scarce. There are several species of hook-fruited *Geums* in which the silky hair of the carpel is continued part of the way up the style, e.g., *G. rivale* and *G. pallidum* (here the style is hairy to the tip, but also hooked).

G. heterocarpum, of the Mediterranean region and Asia Minor, has a few large carpels with rather stiff straight spines with extrorse hairs by which they are probably attached to passing animals.

Streptogyne is a genus of two species of jungle grasses with the usual broad leaves of such plants, and a long unilateral spike of very narrow spikelets, 1 to 1¼ inches long, from which projects a style ½ an inch long furnished with sharp downward-pointing barbs, persistent in fruit, with the tips spirally revolute, and usually those of 2 or 3 spikelets twisted together. One species occurs in Mexico, Trinidad, Guiana and Brazil, and the other, *S. gerontogea*, in West Africa, Travancore and Ceylon. It appears to be very adhesive with its long persistent barbed styles. Chipp says, in Africa:—"Fruits catch in "the hairs of men's legs and are very painful," and Lane-Poole describes it as a grass with hooked seeds which attach themselves to the hairy legs of dogs, harness, antelopes, etc. (Pl. XVIII, fig. 16).

Polygonum virginianum (*Polygonaceae*).—A tall woodland species of North America with a slender raceme over 12 inches long, erect, and numerous solitary flowers a short way apart. The achene, when ripe, still retains the 2 long styles, now rigid and hooked at the tip. They would be readily attached to passing animals. It grows by streams in woods. To some extent it appears that the plant is also dispersed explosively (*see under* Explosive Fruits, p. 672). I failed, however, to produce this explosion in plants grown at Kew, though the ripe achenes fly off rather quickly when the raceme is shaken.

Zannichellia palustris (*Naiadaceae*).—This water weed is common and widely dispersed. Guppy (in *Science Gossip*, 1894, p. 146) says that its long-beaked fruits can entangle themselves in the plumage of water-birds and so be disseminated. The plant is very widely dispersed, and occurs very conspicuously in isolated lakes and pools. Thus I find in Kew Herbarium specimens from Garnet Pool, Malvern, Duddingston Loch, a pond near Rowland's Castle, Hants, one near a farm at Ruislip Mill, pond at Barwesford, Northumberland, one in Orkney, and in Cuyamarca Lake, 4,000 feet altitude, California, etc., strongly suggesting transport by birds. It is widely distributed over Europe, temperate Asia, India, South Africa, Madagascar and Rodriguez, Egypt, Sahara, North America to Guatemala, New Zealand (1847), and on islands such as Malta, Karek Isle, Persian Gulf, Canaries, Liukiu. It is absent from Australia and all tropical countries (Pl. XVIII, fig. 15).

Spiny and Hooked Fruits.

Fruits in which the pericarp is provided with spikes or hooks for adhesion are much more abundant than those which have modifications of bracts, branches, calyx or styles for dispersal by attachment. In many cases the

fruits of herbaceous plants are hairy, and they are often provided with short processes, the object of which seems to be to act as anchors when the fruit is drifted along by rain-wash or wind. These hairs or processes may be so developed as to act as attachment-organs to fur, cloth, or plumage. Plants so dispersed belong to many orders, but chiefly herbaceous ones, as these low plants more readily come in contact with passing animals. They are also mainly desert or steppe plants.

In the case of the *Compositae*, and in other orders with inferior fruit, the hooks or spines on the body of the fruit are really outgrowths of the closely-investing calyx-tube, but I have classed them here for convenience.

A number of the small *Cruciferae*, herbs frequenting the desert regions from the Mediterranean to Persia and Central Asia, possess various adaptations in their fruit for adhesion to passing animals. The fruit is in most a 1-seeded indehiscent capsule. *Euclidium* has small oval fruits with a stout hooked persistent beak. In *E. syriacum*, ranging from Hungary, through Persia, to Soungaria, the body of the fruit is covered with sharp spines which, aided by the hooked beak, make it adhesive. In the much more local *E. tataricum* the fruit is merely dotted, and the beak not persistent.

In *Carrichtera Vellae* the valves of the capsule have 3 or 5 ridges of sharp spines on the back of each. This is abundant on roadsides, edges of fields, and rocky places in Southern Europe, the Canaries, and Palestine. It has appeared in England as an alien more than once.

Succowia balearica, a tall branched herb 1 foot tall, has fruits covered entirely with spines, and a long stiff beak. It is found in Algiers, Spain, and Sardinia and Corsica.

Clypeola jonthlaspi, a common little herb in Southern Europe, has small round disc-like fruits, sometimes hairy and readily wind-dispersed. In *C. eriophorum* the hairs are long and woolly, it being even better adapted for wind-dispersal. These are both South European. But the species of Persia, Assyria, Beluchistan and Afghanistan, *C. echinata* and *C. lappacea*, have these hairs developed into spines. *C. cyclodonta* has rather larger fruit, in which the edge of the disc is cut into oblong, truncate teeth like cog-wheels. The hairs on the flat surface of the disc are more sparse, and hooked. The first plant of this species found was discovered by Delile at Montpellier, where it had been brought in wool (*Bull. Soc. Agric. Herault*, 1830, p. 257). It was later discovered to be wild in Algiers.

We have a somewhat similar case of transformation from a wind-dispersed fruit to an adhesive one, in North America, in the genus *Thysanocarpus*, which is allied to *Clypeola*, in which all the species are smooth and evidently wind-dispersed except *T. pusillus*, in which the flat round fruit is hairy-spiny like that of *Clypeola echinata*.

With these may be compared *Calligonum murex* of Mongolia (*Polygonaceae*). Most of the desert shrubs of this genus have the achene winged, much after the style of a Dock (*Rumex*), but some have the wings covered with branched elk's horn processes, which add to their lightness. All these are dispersed by wind, blowing across the steppes and deserts. In *C. murex*, however, these elk's-horn processes instead of being soft and slender, are rigid and sharp-pointed, so that the fruit adheres readily to a passing animal; the same metamorphosis from a wind-dispersed plant into an adhesive one, by modifications of the processes originally destined to aid its flight in the wind (Pl. XIX, fig. 11).

Triumfetta (*Tiliaceae*).—A large genus of usually weedy, twiggy shrubs about 2 or 3 feet tall, found abundantly all over the tropics. There are a large number of species, which, if grouped by their fruits, fall into 3 sections: (1) creeping sand-shore plants with rather large, round spiny capsules, the spines short, stout and not hooked (these are mainly sea-dispersed, and range

from Polynesia westwards to Siam); (2) larger erect shrubs with globose capsules covered densely with plumed but not hooked bristles (these are natives of open country in Africa and Australia, and are evidently disseminated by wind); (3) weedy shrubs, erect, usually 2 to 3 feet tall, with thin-walled capsules, smaller, or as much as 1 inch across, and densely covered with very adhesive hooked and sometimes also hairy bristles. These are animal-dispersed, and the most abundant all over the tropics. The most widely-distributed species is *T. rhomboidea*, a weedy, twiggy few-branched plant about 3 feet tall, with little yellow flowers in axillary clusters, and small globose capsules about ¼ inch across, tomentose, and covered with short hooked spines, indehiscent, and containing 4 seeds (Pl. XIX, figs. 1 and 2). This plant is extremely common in waste ground about villages, by roadsides, and is to be found all over Africa, India, Ceylon, China, Formosa, Malay Peninsula, Java, Borneo, Timor Laut, Amboina, Philippines, New Guinea, Australia (in 1914, probably recently introduced), Samoa, New Hebrides, New Caledonia (introduced) and South America. It is absent from oceanic islands.

The species has been made into a considerable number, but may be considered to be one very variable species. Its original home is probably in Africa, as not only does it appear to occur in land unaltered by man, but it varies into a great number of forms, whereas in other countries one finds but one or two variations. Its spread throughout the world is undoubtedly due to human agency, as its small indehiscent hooked fruits readily attach themselves to cloth. The larger-fruited species, though apparently occasionally carried about by man, are more likely to be removed from the clothes (when attached) at once, while the smaller ones are liable to be overlooked. The open dehiscence of the larger ones causes the smooth seeds to fall out directly, but, as the whole bunch comes off *en masse*, some of the fruits have not dehisced, and may dehisce as the bearer walks along, and, besides, some of the seeds may get caught in the tangled mass of hooked spines.

Birds are not likely to come into contact with these weedy village herbs, so that they would hardly transport the seeds of such plants as *T. rhomboidea* to distant islands; and, in fact, we find this class of *Triumfetta*, very common though it is on the mainland and large inhabited islands, is absent from oceanic islands.

Several species, however, with larger dehiscent fruits, such as *T. cana*, *T. pseudocana*, etc., are more widely dispersed. One worth recording is *T. suffruticosa*, a bush with fruits 1 inch across, strongly hook-armed, which by clinging together form a mass 3 or 4 inches long. It is a native of Java, Borneo, Solomon Islands, Louisiades, and Timor Laut. This is not, apparently, a native of cultivated land, and does not owe its dispersal at all to human agency. I found it in fruit in Christmas Island in some quantity in one spot, far away from any human habitation, and discovered, when I got back to the Settlement, after a long walk through the woods, that a large bunch of the fruit, 3 or 4 inches long, had attached itself to the back of my coat and retained its hold during the whole march. There can be no doubt that this plant owes its arrival at Christmas Island to its adherence to the body of some large bird, probably a sea-bird, which had, previous to flying to the island, seated itself in a bush of the plant. It is due to the fact that this plant forms a bush on which a bird can sit, that it has been carried about to the islands. The slender, twiggy, unbranched stems of *T. rhomboidea*, *T. cana*, etc., a bird cannot sit on, and, unless it flew very close to the ground through a number of these plants in fruit, could not possibly come into contact with the capsules.

T. procumbens.—This is one of the section mentioned first as mainly being sea-dispersed, and the fruits not only float, but are carried about in floating

pumice. Guppy states he is informed by Mr. G. C. Ross that he has found these prickly fruits attached to the feathers of boobies, the soft investing spines with recurved points well adapting themselves to this aid in dispersal. This class of *Triumfetta* inhabits sandy shores by the sea.

Urena lobata (*Malvaceae*) is like *Triumfetta*, a weedy, wiry shrublet, with 5 separate 1-seeded carpels covered with hooked spines (Pl. XIX, figs. 3 and 4). It is very common in waste ground and roadsides all over the world, and is probably an original habitant of Africa, where it is common and variable. It is found also in the Cape Verde Islands, all the Mascarene Islands, and Madagascar, India, China, Formosa, the Malay Peninsula and all the Malay Islands, including the Natunas, most of the Polynesian Islands, and Cook Island near New Zealand, in Australia (rare, and not recorded before 1870), Florida, and the South American continent to Paraguay, including Fernando de Noronha and the West Indies; but it is absent from oceanic islands not inhabited by man. Its little hook-armed carpels stick very tightly to clothing and animals' fur, and it owes its wide distribution undoubtedly to this. The beautiful *U. rigida*, with non-spiny carpels, occurs only in Burmah, Siam, and Borneo. The absence of this common plant from oceanic islands not invaded by man or large mammals suggests that the fruits are exclusively dispersed by these and not by birds.

Tribulus (*Zygophyllaceae*).—These are small creeping or erect plants inhabiting dry country or deserts, seashores, arable land and inland sand-hills. The fruits are usually 5-angled, of 5 cocci, each containing 1 seed, and strongly armed on the backs with spiny or tubercled wings. *T. macropterus*, a desert plant, is hairy and hardly spined. It is evidently dispersed in the sands simply by wind. Of the rest, the carpels are generally strongly spiny, each carpel being separated when in fruit. These spiny carpels readily attach themselves to the foot of any animal treading on them (Pl. XIX, fig. 5).

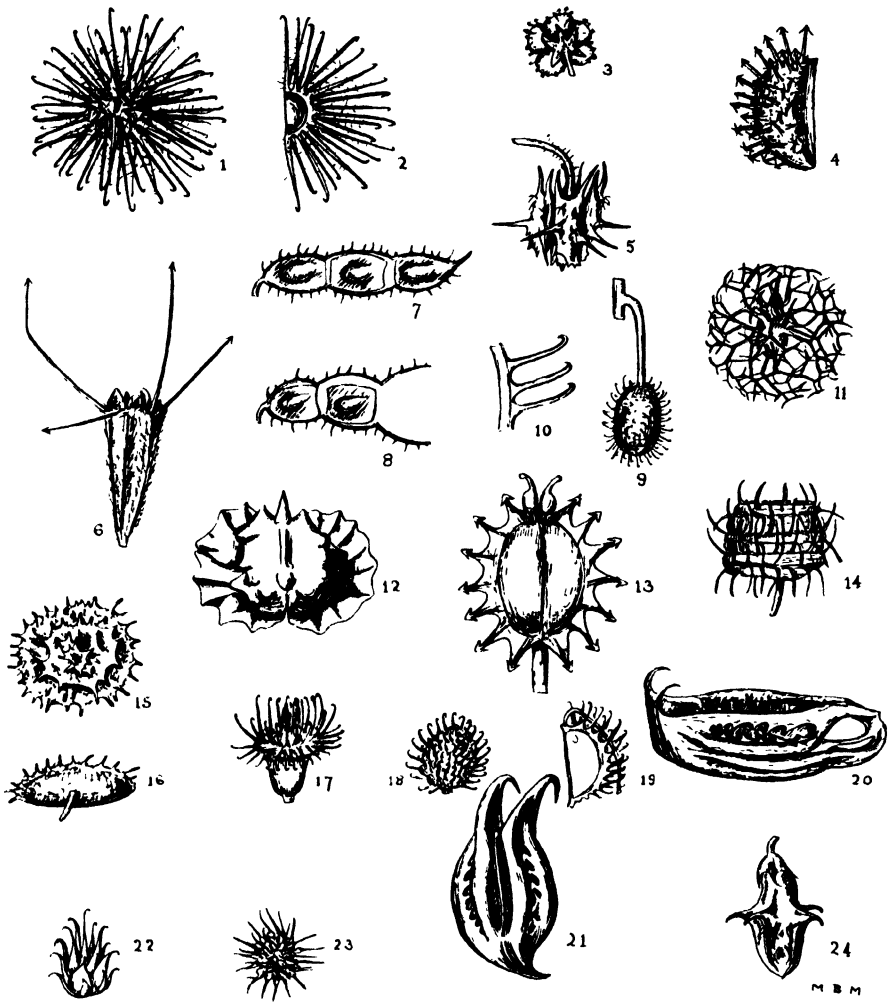
Kerner writes:—"One of the species, *Tribulus orientalis* (*T. terrestris*), is "of common occurrence in the lowlands of Hungary, and is an object of "dread to the shepherds of that region. The fallen segments into which the "fruit resolves itself are armed with hard, sharp, and comparatively long spines, "and are often covered with drifted sand, so that only the tips of the spines "project above the surface. These prickles pierce deep into the hoofs and "soles of the animals that tread upon them, and are broken off the fruit by the "efforts to rid them of the impediment."

Burtt-Davy (in "Alien Flora of the Transvaal") says that these burrs stick in the feet and wool of sheep and kids. Mr. Burtt describes their attachment to human feet, and to the tyres of motor-cycles and motor-cars in great numbers, so that nowadays they may be transported very many miles in a day.

Dell and Bryan, in an expedition to Laysan Island, Hawaii (*U.S.A. Agric. Bull.* 42, 1912) write:—"On the foot of a Laysan Albatross (*Diomedea immutabilis*), between the toes, was a spinate seed about as big as a buckshot, *Tribulus hystrix*."

According to Guppy, these cocci do not float in water, and so cannot be dispersed by sea-currents. This being so, we are reduced to the theory that its presence in islands where it is common on seashores must be due to its transportation by birds. Its dispersal on continents may well be due to the adhesion of its spiny cocci to the feet of animals. The most common species seems to be *T. cistoides*, but *T. terrestris* (and some other described species which seem to me merely local forms of it) is remarkably widespread and often very abundant. *T. terrestris* and its forms are found in Europe, Africa, Siam, China, and in Little Kei, Timor Laut, the Philippines, Formosa, Hainan, Australia (1802), Rocky Islet, near the Gulf of Carpentaria, Booby Island, New Caledonia, Mackean's Island, Phoenix Group, Oahu, Clarion

PLATE XIX.



ADHESIVE FRUITS, ETC.

FIG. 1. *Triumfetta oblonga* (fruit, enlarged).
,, 2.— ,, ,, (single loculus).
,, 3.— *Urena lobata* (fruit, enlarged).
,, 4.— ,, ,, (single loculus).
,, 5.—*Tribulus terrestris* (fruit).
,, 6.—*Acaena variabilis* (fruit).
,, 7 and 8.—*Mimosa pudica* (fruit).
,, 9.—*Circaea lutetiana* (fruit).
,, 10.— ,, ,, (hooks, enlarged).
,, 11.—*Calligonum caput-medusae* (fruit).
,, 12.—*Pretrea zanguebarica* (fruit).
,, 13.—*Drusa oppositifolia* (fruit, enlarged).
,, 14.—*Medicago arabica* (fruit, enlarged).
,, 15 and 16.—*Neurada procumbens* (fruit from above and from side).
,, 17.—*Agrimonia Eupatoria* (fruit, enlarged).
,, 18.—*Sanicula europaea* (fruit).
,, 19.— ,, ,, (one mericarp).
,, 20 and 21.—*Martynia annua* (fruit).
,, 22.—*Remusatia vivipara* (bulb, enlarged).
,, 23.—*Barclaya Motleyana* (seed, enlarged).
,, 24.—*Pedalium murex* (fruit).

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and Bird Isles, Isle of Pines, Hawaii, St. Helena, Socotra, Cape Verde and the Canary Isles. In North and South America, as far as the Argentine, it occurs usually inland and by roadsides, probably introduced, as it is recorded as having been imported into Colorado in ballast. In Galapagos Island (where also a spineless form is found) it was probably carried by birds.

In some of the *Leguminosae* the pod is similarly armed with sharp thorns, which may, perhaps, by attaching itself to the foot of a passing animal, be conveyed to some distance. One of these is *Sindora*, of which the pods of all species but one are armed with sharp prickles, from the tip of each of which a small quantity of a sticky resinous gum exudes. The pod is 1-seeded, and dehisces after falling, and the single seed remains attached by a yellow waxy funicle to one valve. This funicle is eaten by rats, as described under Arils (*see* p. 427). It seems very probable that the spines may penetrate the foot of a large passing animal, and the valve with the seed attached, or the pod before opening, may be carried to some distance from the tree. The species with the unarmed pod, *S. coriacea*, has the whole pod, when ripe, very resinous and sticky. The trees, of great size, are natives of the Malay forests.

Glycirrhiza lepidota.—This shrubby leguminous herb of North America and Mexico has flat ellipsoid 1-seeded pods, about ½ inch long, strongly armed with stiff hooked spines. They are borne in a dense raceme about 3 inches long. R. Miller Christy (in his " Notes on the Flora of Manitoba ") records that he found numerous pods of this plant adhering to the buffalo robes exposed for sale. The so-called buffalo is, of course, the American bison. The pods were fixed chiefly in the long hair on the chest, hump, head and tail of the animal. The American bison must have carried about the country in its wanderings very many of this class of armed fruits (*Desmodium*, etc.). An account of the plants it carried in mud on its hair is found under " Seeds and Fruits Conveyed in Mud " (p. 536).

G. echinata, a similar plant, native of Eastern Europe and Asia Minor, as far as to China, has armed pods, but the spines are not hooked as in the previous species.

Desmodium is a very widely-distributed genus of herbs or shrublets, some few forming bushes about 6 feet tall, in which the pod is jointed and breaks up into segments, each containing 1 seed. The joints are usually flat, narrow at both ends, more or less square, or cuneate or linear-oblong. They are generally hairy—at least, on the outer edges—and frequently covered on the faces with very short viscous hairs, so that they are readily adhesive to clothes, or fur or plumage. (In a few plants, e.g., *D. umbellatum*, usually separated generically now, the fruits are not adhesive.) The genus is a very large one containing many species, and is chiefly tropical or subtropical. It is absent from Europe and temperate Asia, except for one species (probably recently introduced) from New Zealand, but is found all over the rest of the world, including the temperate regions of North America. These plants are absent from oceanic islands, except Galapagos, where there are 5 species, 1 endemic, and there are 4 in Fernando de Noronha, but none endemic, and all probably introduced. Though abundant in Java, no species had reached Krakatau by 1919.

These plants usually occur in grassy plains and open woods, and in tropical forests along the paths made by wild beasts and man. The joints of the pods are certainly very adhesive in the smaller species, but the larger bushy ones, such as *D. megaphyllum*, have non-adhesive fruits. In North America these plants are popularly known as Tick-Seed (*Desmodium acuminatum*), Tick-Trefoil or Beggar's Lice (*D. canadense*), Tick Plant (*D. nudiflorum*), from the adhesion of their small joints to clothing. Gunn writes of *D. gunnianum*, of Australia :— " The joints adhere to your fingers and to any substance." The most

persistently adhesive are those in which the very short hairs on both sides of the pod are hooked, such as in those of *D. zonatum* (*D. ormocarpioides*), of Malaya, and *D. adhaerens*, of the further eastern islands from Celebes to Papua. The former is not rare along jungle paths in the Malay forests, and is clearly transported from place to place by the wild beasts which traverse the forests by these paths. In the same localities we find the more widely-distributed *D. gangeticum* ranging from Africa to India, Malaya and Polynesia. These are all slender shrublets with long thin racemes of rather distant flowers, which, when in fruit, easily reach the legs of a passing deer, tiger, or other rambling beast. *D. polycarpum* is an open-country species in which the pods are rather crowded, the flat joints are strongly armed with rather long hooked hairs on the edge and a few smaller ones on the sides. It grows all over warm and tropical Asia, China, India, Malaya, Australia and Polynesia as far as Hawaii, and has been found in Cook Island in 1899. Hillebrand says of its presence in Hawaii :—"It is called Spanish clover, and was introduced from Chile, a "good fodder." It does not, however, occur in Chile or any part of South America. It must have been introduced from tropical Asia. It is possible that this has been carried about as a fodder plant by man, but more likely attached to the hair of buffaloes or goats. I have never known it cultivated.

D. triflorum is a small flat creeping plant in grass which is now all over the tropics, and the very similar *D. heterophyllum* is common in parts of Asia. The little adhesive joints of the pod can only be attached to animals' feet as they lie almost hidden in the grass. Of course it is locally carried about in turf, as it is found in all lawns, but probably also on the feet of cattle, and perhaps on rats or other small animals.

The complete absence of all these *Desmodiums* from all islands except Galapagos, unless brought by man, seems to show that birds play no part in their dispersal.

Zornia diphylla, like *Desmodium*, has pods which break up into joints, but these are rounder, and armed on both faces with short, sharp, erect spikes. The little plant is prostrate, and the joint of the fruit quite small. It can only be dispersed by animals treading on it and picking up the joints on their feet. It is found all over Africa, India, China, Malaya, and Australia (though scarce here), and South America, including the islands of Fernando de Noronha and Galapagos. Except in the latter island, it seems to be absent from islands unless inhabited by man, and the fruit is probably carried about on the feet of goats and cattle, as in *Mimosa pudica*.

Scorpiurus.—The caterpillar plants are annual herbs of the Mediterranean and Asia Minor regions, in which the pod is curled and often provided with sharp short spines on the back. The pod is not so lightly coiled as in the medick, and it is not so well adapted for adhesion. *S. vermicularis* is densely covered with short blunt processes with a dilated top, apparently viscous. It is rather tightly curled, and ¾ inch across. It is found in Spain, Morocco, the Canaries, and Madras.

In *S. muricata* and *S. subvillosa* the pod is less curled, and bears numerous short, stiff, acute spines on the back and ribs, and in *S. subvillosa* some of the spines are hooked. They are found all along the Mediterranean to Egypt, Palestine, Mesopotamia, and *S. subvillosa* to Abyssinia and Erythroea, also in Madeira and the Canary Islands. Less well adapted for dispersal by sheep or cattle both by their armature and by their being rather more of desert and sand-hill plants, their area of distribution is very much more limited. Lubbock (" Flowers, Fruits, and Leaves ") suggests that the resemblance of these fruits to caterpillars may be to induce birds to mistake them for these insects, and to carry them for some distance before they find out their error. This is very

improbable, as a bird would hardly be deceived by this curious and quite accidental resemblance.

Medicago.—The Medicks are herbs of the European and North Asiatic region. The pods are usually curled into a spiral ball, which is generally armed along the edges with sharp or hooked spines, by which they adhere readily to fur, wool, or clothing.

M. denticulata pods have very numerous slightly-curved spines. It is abundant in Europe, Asia Minor, India, Egypt, Abyssinia, Socotra, Canaries, Madeira, the Cape (before 1854), California (1833), Bermuda, Brazil (1875), Chile (1820).

M. arabica is found in Europe, Algiers, Canaries (rare), Palestine and the Cape (but rare here), North America, New Granada (1851–1857), Juan Fernandez (1873), Chile. In this the spiral ball is rather large, with about 3 whorls of sharp straight spines running horizontally from the edges. The plant is more sporadic than in *M. denticulata.* It usually grows along path-edges. It appeared in some abundance in an old football field near Mortlake one year, when the turf was ploughed up for allotments. I suppose that the seed had been lying in the soil for many years, as I could find it nowhere else in the locality.

M. minima has small fruits ⅛ inch long, with hooked spines, and is common in Europe, Asia Minor, through Persia to India, Madeira, Canaries, Socotra, Africa, Australia and South America. The small size of the fruits gives this an advantage over the other species, as it is less likely to be detached from wool (*see under* Dispersal by Sheep, p. 601). *M. echinus*, absent from England, has fruits 1 inch long, a perfect ball of bent spines. It occurs in Europe and North Africa, Asia Minor, Syria, Madeira and the Canaries.

M. tribuloides.—In this plant the spines vary from short, curved, stout, acute processes to long decurved ones. It occurs in the Mediterranean region to Arabia and Madeira and the Canaries.

M. helix has two forms. In one the pod is quite unarmed and rather thin and flat, so that it may be readily dispersed by wind; in the other the edges of the spiral are spiny and adhesive. It is found in the Mediterranean region, Madeira and the Canaries. Both forms seem to grow together.

There are several other spiny adhesive species in the Mediterranean region, but it is noticeable that very many of the species inhabiting the Algerian deserts are not armed, but apparently drifted by wind only, while in the Canaries the majority are armed with adhesive spines. The most widely distributed, with two exceptions to be mentioned below, are all spiny-fruited plants common in the temperate regions of Europe. There is little doubt that these plants have been dispersed by their attachment to the wool of sheep and goats, and thus carried to the islands. The two widely-distributed species not armed, are—*M. lupulina*, Europe, Asia, India and Mongolia, Arabia, Canaries (rare), Madeira, North America, Bermudas, Bolivia (1890); and *M. sativa*, the Alfalfa on Lucerne, which is probably a native of Mongolia, and has been carried as a fodder plant, and planted all over the world. *M. lupulina* has been carried *as* a fodder or accidentally *in* fodder; locally it appears to be dispersed by birds and water. Gerard mentions *M. sativa* as cultivated for fodder on the Continent, and says:—"We have a little in our gardens (1633)," so it appears to have been introduced into England about the 17th century. It was, however, introduced into Europe from Persia at the invasion of Greece, 424 B.C., as a horse fodder by the Persian army.

Mimosa pudica.—The Sensitive plant is a low, shrubby, spiny plant, well known for the peculiar and striking movement of its leaves and leaflets when touched. The thin flat pods are armed along the sutures with sharp bristles. They are from ½ to 1 inch long and ⅛ inch across, and have from 1 to 5 joints, each containing a single seed. These fruits are borne in heads. When quite

ripe, the joints fall out separately, leaving the sutures intact. The joints themselves are not armed (Pl. XIX, figs. 7 and 8). The pods are readily attached to clothing or the fur of animals, and are especially noxious to cattle and sheep, as they get between the toes of the animals and produce serious sores. They break off when trodden on, before the seeds fall from the sutures, and, being carried along by the animals, shed the seed-joints as they go. The plant is a native of South America, and was introduced into the Old World in the 16th century, apparently solely as a curiosity, for it neither has nor ever had any reputation as an economic plant of any value. Shortly after the discovery of America, the Jesuit missionaries contrived to import useful plants from South America and the West Indies to their Settlements in Manila, and thence to Goa, and from these spots many of the South American weeds and useful plants were spread over tropical Asia, and in this way there can be little doubt that the Sensitive plant arrived in the Old World. It is now common in India, Annam, Siam, the Malay Peninsula (1830), Java, Borneo, Amboina (1750), Philippines, New Caledonia, Samoa, West Africa, St. Thomas and Prince's Isle, Zanzibar, Rhodesia, as well as all parts of tropical America. In some of these places, however, especially in Africa, it seems to have spread very little, and in many places it has been introduced into botanic gardens, and spread thence. Some years ago a Chinese servant brought a plant from Singapore to Sarawak, Borneo, being much struck by its closing its leaves on being touched, but his master, knowing how injurious it would prove to cattle and goats, seized it and destroyed it. The plant, however, had already been brought in some such way to Borneo. It frequents open country, roadsides, and damp pastures. No animal will eat it, as, when they touch it, the leaves close, leaving only the thorny stems; and dogs will not walk through it, but spring over it when they come across it. Hence it is by no means as widely dispersed as it might be. Several of the other species of *Mimosa* have spiny pods, notably *M. polydactyla*, of Guiana and Brazil, a 6-foot bush, and *M. acanthocarpa*, of Mexico, apparently also a bush. These have not spread like the sensitive plant. They do not seem as sensitive, and probably were thus not so attractive as a curiosity, and the low-creeping habit of *M. pudica* again makes it more easy to spread and more difficult to exterminate.

Acaena (*Rosaceae*).—A genus of plants allied to *Sanguisorba* (which, except in the fruits of most species, it much resembles) herbaceous or half shrubby at the base. The flowers are in heads, globose, or spicate; in one set of species the calyx in the fruit is armed with sharp spiked sepals; in the others the sepals are oval, and foliaceous, but the calyx-tube is armed with hooked spikes. In many species the spines are armed at the tip with 1 to 3 sharp recurved points, making them like small grapnels. In one or two species there is no armature at all, e.g., *A. microphylla* and *A. inermis* of New Zealand, and *A. exigua* of the Sandwich Islands. The *Acaenas* are Antarctic, a few in Australia, many in New Zealand, the Falkland Islands and South America, and some occur in the Atlantic islands.

A. sanguisorbae, with heads ½ inch through, has 4 needle-like sepals, the calyx-tube being hairy. It occurs in Australia, Tasmania and New Zealand, and Macquarie Islands.

A. ascendens, which much resembles it, has 2 reflexed grapnel points on the tips of the long sepal-spines. It is found in New Zealand, the Falkland Islands, Kerguelen and Marion Isle. *A. sarmentosa*, of the same affinity, is a native of Tristan d'Acunha. There can be no doubt that these plants owe their presence in these islands to sea-birds, for the grapnel spikes are calculated to adhere strongly to birds' downy plumage, but they have also been brought in sheep's wool to Tweedside. *A. lappacea*, of Colombia and Peru, has the fruits spiny all over, the spines with deflexed grapnel points. A collector in Kew

Herbarium notes: "The seeds are troublesome to travellers (barefooted)." *A. myriophylla*, of the *A. sanguisorbae* type of fruit, occurs in South America, and G. Claraz writes a note saying that in Bahia Blanca it grows especially round the burrows of the Viscachas (*Lagostoma*), by which rodent it is doubtless carried about.

In *A. cuneata*, of Patagonia, the sepals play no part in the dispersal, as they are foliaceous and not spiny, but the tube of the calyx is covered all over with short, rather stout, grapnels; and *A. coespitosa*, of the same region, is similar, but the grapnels are arranged in longitudinal ridges of the tube (Pl. XIX, fig. 6; Pl. XX, figs. 5 and 6). Similar to these species are *A. ovalifolia*, found in Hermite Island, Cape Horn, Chile and Juan Fernandez, and *A. argentea*, also found in Chile and Juan Fernandez. Of this species C. Skottsberg writes (in the "Natural History of Juan Fernandez," ii):—"We found the achenes "of *A. argentea* in the down of a *Pterodroma* (a kind of petrel)."

A. ovina has globose heads of fruits with sharp sepaline spines in every direction. It is found in Australia and Tasmania, and has been introduced into New Zealand. A. Cunningham, in a note in Kew Herbarium, writes:—"I wish it a rarer plant than it is, when I find my sheets and clothes have been "dried on it, as the seeds are a perfect antidote to rest, being as sharp as pins, "and adhere to anything they touch." Thomson (in "Naturalisation of Animals and Plants in New Zealand") says it is spread by sheep in New Zealand. Capt. Carmichael, in speaking of the Tristan d'Acunha species, says that it overruns the low ground, and the fruit fixes itself into one's clothes, on the slightest touch, and, falling into a hundred pieces, covers one all over with an unseemly crust of prickly seeds, not to be got rid of without infinite labour (*Trans. Linn. Soc.*, xii, 483, 1818). Here what he calls "the fruit" is the *head* of fruits, and the "prickly seeds" are the separate fruits. Moseley, Kidder, and others refer to the burrowing habits of the petrels, puffins, and other sea-birds among the vegetation covering the ground in the Atlantic islands, and Moseley states that the fruits stick like burrs to feathers, and as he says that the petrels and other sea-birds burrow and breed high up in the mountain slopes of tropical islands like Hawaii, this, as Guppy points out, would account for the presence of *A. exigua* on the tops of the Hawaii mountains where it occurs, though this locality is far away from the area of dispersal of the genus, which is otherwise absent from Polynesia.

Some of the species are cultivated as rock plants in England, and *A. sanguisorbae* has migrated as far as Hey Tor, in Dartmoor, the fruits carried, no doubt, from some garden by birds, rabbits, or some other animals.

It is curious to find that in one genus we have adhesive apparatus formed of two separate organs, in one series the sepals are converted into spines with grapnel-points, and in the other the grapnels are apparently a modification of the hairs clothing the tube of the calyx. The dispersal of the insular plants of this genus is undoubtedly due to sea-birds, while the abundance and wide distribution of the mainland species, notably in South America, is due to adhesion to the fur of wild animals, such as Viscachas, and also to domestic cattle, sheep, etc., and to human clothing.

Neurada procumbens (*Rosaceae*) is a prostrate desert plant of North Africa from Algiers, through Egypt to Palestine, Arabia and Scinde, and in Nubia, reappearing in Herreroland. The fruits are round, depressed-conical, flat below, and the edges are armed with strong hooked spines, the styles are also spiny. It consists of 10 carpels, connate and enclosed in the spiny calyx. The carpels, which contain 1 seed each, dehisce above. It doubtless is distributed by attachment to the feet of large animals, and possibly by the wool of sheep lying on it. Massart records it as one of the very few plants with adhesive fruits occurring in the Algerian Sahara (Pl. XIX, figs. 15 and 16).

Agrimonia.—The Agrimony *A. Eupatoria* is a well-known English herb, with a tall raceme of yellow flowers and pendent bell-shaped fruit, armed at the top with a number of stiff curved bristles hooked at the tip, which spring from the tube just below the sepals. These fruits contain 1 or 2 seeds, and are very adhesive to fur of animals and cloth. The plants grow frequently by roadsides, where the fruits become attached to and borne off by passing animals, such as dogs or sheep, or to human clothing, and also frequently occur in pastures, where they are probably carried by cattle or sheep. A number of species have been described, but they are all closely allied, and nearly all at some time have been classed as belonging to the English species *A. Eupatoria* (Pl. XIX, fig. 17).

They are very widely distributed over the north temperate region, running down the mountain chains in the tropics. *Agrimonia* occurs all over Europe, North Asia, India, Ceylon, Java, China, Japan, Sachalin, South Africa, the Canaries, Madeira, Azores, Algiers, North America to Mexico, and in Brazil, but here doubtless introduced by man, or perhaps by cattle or dogs. It seems improbable that birds play any part in its dispersal.

Circaea lutetiana (*Onagraceae*).—This abundant woodland herb, which is found in damp shady spots, has soft green fruits, usually 2-seeded, covered with hooked hairs, which very readily adhere to fur or clothing. They are borne on long pedicels on a slender raceme, so as to spread widely. The few species occur in Europe, temperate Asia, China, Japan, and North America. These fruits are distributed by their attachment to the fur of small animals, such as rabbits or cats. The Rev. Dr. T. S. Lea told me that a cat used to bring them into the house, and that he could tell when it had been sleeping on his bed, by the presence of these fruits. In my garden it is abundant in two places where the cats constantly go, though I do not know any nearer wild locality for it than Petersham, some miles away. Many years ago this part of Kew was open country, and probably the plant grew nearer here, and was brought from the wild country into the garden, where it still remains. The fruits are recorded by Woodruffe-Peacock as travelling by adhesion to human clothes. Indeed, everyone walking through our woods in summer knows this. (Pl. XIX, figs. 9 and 10).

Sicyos angulatus (*Cucurbitaceae*) is a slender bryony-like plant, with small globose fruits about ½ inch through, densely covered with barbed spines, which are the means of attaching them to animals and so dispersing them. Its distribution is somewhat peculiar. It is abundant in North America, whence, doubtless, it has been carried to the Mediterranean region, where it is now found in the Tyrol and Balkans. It has also been met with in Abyssinia and Angola. It appears to be quite absent from South America and the West Indies, except that it has reached Bermuda, but is common in Australia, where it was found by Robert Brown in 1802 to 1805, and in New Zealand, collected by Sinclair in 1824, Kermadec (1854). Cogniaux separates this Australian plant from the American, but the two plants are quite similar. The remaining species of the genus are found only in America and the Hawaii Islands. There is no doubt that it has been diffused in Australia, New Zealand, and Kermadec Isles, by adhesion to the wool of sheep.

Sanicula (*Umbelliferae*).—This is a large genus of 39 species of woodland herbs, perhaps one of the most widely distributed of all umbelliferous genera. The species all have small heads of fruits, which in one set are thickly covered with small hooked spines, while the others are not so armed. The spiny-fruited kinds are widely dispersed throughout the world, while those with smooth fruits are very local. The plants are about a foot tall, and the small spiny fruits can attach themselves readily to the fur of small animals like rabbits or foxes, or the ground birds, as well as to human clothing, though

I doubt, from the abundance of these plants in little-frequented spots, whether this latter source of dispersal has played an important part in their distribution.

Every English plant-lover knows well the common Sanicle (*Sanicula europaea*), which is so abundant in English woods, and might be surprised to find it equally plentiful in many mountain woods in the tropics. It is, indeed, the most widely-diffused species in the genus, and is one of the few English plants to be found in the Malay Peninsula. It occurs also in India, Ceylon, Persia, Siberia, China, Japan, Burma, the Malay Peninsula, Sumatra, Java, Celebes, the whole of Africa from Morocco and Abyssinia to the Cape, Madagascar and the Comoro Islands (Pl. XIX, figs. 18 and 19).

A closely-allied species, *S. azorica*, is found in the Azores; several allied species *S. canadensis*, *S. liberta*, *S. marylandica* in North America and Mexico to Bolivia; *S. patagonica* in Patagonia; and *S. Sandwicensis* in the Sandwich Islands. *S. europaea* is absent from the Canary Islands, Madeira, and all oceanic islands. It is largely a continental plant, and there is nothing to suggest that it owes anything in its wide dispersal to human agency, as the plant inhabits woodlands, and does not appear in cultivated ground or roadsides. Birds may have played some part in its distribution, as it would otherwise be difficult to account for the presence in the Azores of *S. azorica*, and of *S. sandwicensis* in Hawaii. This latter, Guppy points out, is an ally of the Oregon species *S. Menziesii*. *S. europaea* is undoubtedly mainly dispersed by mammals. Its low habit and wide straggling branches and small fruits armed with hooks adapt it for such a dissemination.

The genus obviously originated in the north temperate region, and was common to what is now called the Nearctic and Palaearctic area, being transported southwards from the Mediterranean region, along the African mountain ranges, to Western Africa and to the Cape, from the Himalayas to the Nilghiris, and to Burmah, to Java and Sumatra, from Sumatra to the Malay Peninsula and Borneo, while modified forms spread in like manner from the Nearctic region south to Patagonia. The Sanicle inhabits open woodlands in cold or temperate regions at sea-level, and in the tropics it only occurs in similar spots on mountains at a considerable altitude, in the Malay region at from 4,000 to 5,000 feet altitude, and usually in isolated spots. It is only known to occur in one spot in the Malay Peninsula—on the west coast opposite Sumatra. This spot is an isolated patch surrounded on all sides by the dense Malayan forest. With it grow Violets, *Disporum*, and a few other plants of the north temperate region, forming a small patch of exactly the same plants which I found forming a large woodland flora on the opposite coast of Sumatra at an altitude of 5,500 feet. In fact, it was a little island of north temperate plants from Sumatra, left over from the time when the mountains of Sumatra and those of the Malay Peninsula were connected by land, and which had survived when all the remaining parts of the Peninsula had been overflowed by the tropical rain-forest flora of the lowland Malay region. It is in the same way that we find Sanicle in such scattered spots as in West Africa, the Nilghiris, the inland mountains of Ceylon and Celebes, just isolated remnants of a cold or temperate flora which has disappeared from vast areas lying between these spots, by change of climate and environment. It is not due to stray birds flying from one mountain to another, carrying the fruits of this plant attached to its feathers. Were this so, there is no reason why the plant should not be much more abundant on the mountain ranges of the tropics, nor why it should, in these spots, be always associated with other Palaearctic types.

The history of the Sanicle, therefore, amounts to this. Evolved at what date we know not, but perhaps in the Miocene period in the north temperate area, when America was still continuous with Europe, it travelled, by the aid of its hooked fruits attaching themselves to wild beasts, southwards through

a temperate woodland area all over America from North to South, all over Africa and Asia to the most southern parts. Later, changes of climate and alterations of the environment, and the evolution in some parts of a desert flora, in some a wet, rank tropical vegetation, exterminated it in the south, except in a few spots in which it has managed to survive, but where it cannot now spread owing to the complete change of surroundings.

Daucus maritimus, the Sea Carrot, has the fruits of 2 1-seeded carpels, mericarps, strongly armed on the edge and on 4 ridges with stiff spines. It is very probable that this plant owes some of its distribution to adhesion by the spines to birds and animals, but the cultivated form of the carrot has been early and widely spread over the world. The maritime wild form is, I think, to some extent transported by adhesion to birds' feathers. I observed that some of the rocky islands off the coast of Sark were dotted over with the plants of the sea-carrot. These rocks were precipitous to the sea, so that it was not possible for the fruits to have arrived at the top of the rocks by being sea-borne, and the distance of the islets from the coast precluded any likelihood of their being blown across by wind. It is most probable that they were transported by sea-birds. However, the great abundance of the plant on the sea-coasts of Swanage, Guernsey, etc., precludes their regular dispersal on the mainland shores in this way, and here I think wind plays the most important part. Sheep may in some cases transport the fruits in their wool, as we know they do in the case of *D. glochidiatus* and *D. sahariensis*, as shown elsewhere. *D. pusillus* is a much smaller-fruited carrot, widely distributed over North and South America as far south as Chile and Patagonia. It also occurs in the mountains of Hawaii. The fruits here might be bird-transported. It is hardly likely to have been introduced by man. A form of *D. carota*, allied to the sea-carrot, is found in the Azores, and one in the Canaries, where also are two other species of the genus. How far the presence of these plants in the islands is due to human introduction is dubious.

Drusa oppositifolia.—A scrambling herb with the stems covered with scattered stalked glands, and the fruit with 2 wings armed with grapnel-hooked spines on the edges. This plant is confined to the Canary Islands, and is remarkable, as all the other species of the genus are natives of North and South America, and have quite unarmed fruit. It seems probable that formerly the genus was much more widely distributed, and has only persisted in the Old World in the Canaries (Pl. XIX, fig. 13).

Eryngium.—A large genus of dry herbs or half-shrubs with (usually) spiny leaves, occurring in Europe, Australia, and North and South America, in dry sandy or open places. The fruits are usually armed with short upward-pointed spines with 2 or more acute sepaline spines at the top. The spines are evidently destined to act as anchors in sand, as the fruit is blown along in the wind, though it is probably also adhesive. The allied genus *Astrantia*, of the Caucasus and Mediterranean, a soft woodland herb, has also sharp sepaline spines quite readily adhesive, but does not appear to be widely distributed, as it seems confined to Europe and Asia Minor (Pl. XVIII, fig. 10).

Washingtonia (*Osmorrhiza*) is an American *Umbelliferae* with adhesive mericarps. The species, all closely allied, are tall herbs with widely-spreading slender branches, when the fruit is ripe. The pedicels and oblong-linear fruits are armed with bristles pointing towards the tip of the fruit, and borne on the vittae. These stiff bristles readily catch in clothing and hair of passing animals, and the wide-spreading branches ensure their striking against the passer-by. The genus ranges from North America, by New Granada, to Chile.

Caucalis (*Torilis*).—The fruits of all species of this genus are armed with processes and hooks by which they can be attached to clothing or the

fur of animals. The spines are hooked in the small low plant *C. nodosa*, which is common on roadsides, etc., where it is carried about on clothes, hair of dogs, etc.; but in many species the spines are quite straight, and sometimes barbed with numerous short processes. This is the case in *Caucalis latifolia*, which is widely spread over South Europe and temperate Asia. The mericarps are ½ inch long and densely covered with barbed spikes. They are very adhesive, and a number were sent to me from Peshawar by Mr. E. R. Taylor, who found them adhering to his clothing after a march. This plant occurs as a casual in England, but chiefly in cultivated ground, and is probably, in these cases, accidentally brought in cereals. There are a number of species ranging over Europe and temperate Asia and Africa. *C. anthriscus*, a common, small-fruited one, reaches Java, where I have found it apparently wild, but it is probable that it was introduced in vegetable seeds. Several species are found in Madeira, the Canaries and Azores, probably introduced in most cases accidentally from Europe or the African coast. Two allied genera are of interest. *Psammogeton biternatum*, of the Punjab, has fruits similar to *Caucalis*, but the spines in many cases are more softly hair-like. In *P. crinitum*, of Afghanistan and Persia, the spines are modified into soft white hairs, so that the fruits may readily be wind-dispersed, and this modification reaches its maximum in *Choetosciadium trichosperma*, of Syria, where the soft silky abundant hairs on the mericarps would allow it to fly well before the wind. At the same time it is quite possible that these fruits may be dispersed to some extent by adhesion to the wool of sheep.

Galium aparine (*Rubiaceae*), Goose-grass, Cleavers.—This well-known English plant needs no extensive description. The whole of its long trailing stem is armed with hooks, as are the small round fruits. These are bi-coccous, and covered with the calyx-tube which is the part bearing the hooks. The fruits are very adhesive, as is the whole plant, and is distributed widely by human clothing, the fur of animals, and probably by birds, as some, especially the whitethroat, use pieces of it to make their nests. Unlike other species of *Galium*, it is a climber on hedges and bushes, and the hooks with which it is liberally provided were originally destined for this purpose. Traces of hooks on the fruits of other species (*G. Vaillantii*, etc.) are also to be met with, but they apparently play no part in dispersal. The plant is widely spread over the whole of Europe, Canaries, Africa from North to South, and the island of Socotra, India, China and Japan, the Liukiu Islands, America, from Sitka to Chile, and San Juan Isle, California. It is possible that in some of these localities it may have been carried by sheep, but its absence from Australia and New Zealand seems to negative its being dispersed that way. Its occurrence on the islands mentioned may be due to birds. Most of the other species of the genus, many of which are very widely distributed, have quite smooth fruits.

Asperula odorata.—The Woodruff has small round fruits densely covered with hooked spines. The fruit is larger than that of *Galium aparine*, and the hooked spines longer. It is the only species of the genus with armed fruit, and it is the most widely spread, ranging from Europe, through Persia and Mongolia, to China and Japan. It frequents open woods in temperate regions in the same kind of locality as that in which the similarly-armed Sanicle (*Sanicula*) grows, and, indeed, the two plants often grow together. The fruits are very adhesive to clothes and animals' fur, and there can be little doubt that it owes its wide distribution to small woodland-haunting animals.

The Thrift (*Armeria*) (*Plumbagineae*) has small fruits bearing a sepaline parachute, by which they are borne from place to place by wind. At Tillywhim, by Swanage, I walked through a plot of this plant to see whether the short stiff hairs on the body of the fruit would attach themselves to my clothes. Some did so. I returned to the hotel, and, after lunch, walked to the farther end of

the Swanage Bay, a distance of 3 miles, and found that they still adhered. I have found the Thrift with *Plantago maritima* on sandy ground at Delvine, in Perthshire, far away from the sea, on the banks of the Tay. It is difficult to account for their presence there, except for the agency of the oyster-catchers and other sea-birds, which were flying about and apparently nesting there. The only adhesive mechanism of this fruit is the coating of small hairs all over it (Pl. VIII, fig. 2).

The plants of the order *Boragineae* are remarkably suited for dispersal by attachment to animals. They are open-country plants largely, and apt to be scabrid, so that occasionally whole plants or their inflorescences adhere to passing animals, or the calyx is adhesive, or the 4 nucules. In the Hound's-tongue (*Cynoglossum*), the nucules are strongly adhesive. The genus is very widely dispersed over the world, and this is due to the armature of the little fruits. They are rough herbs, 2 or 3 feet tall, with long, simple, or branched and spreading racemes of scattered flowers. The nucules, 1-seeded carpels, are covered with numerous short grapnel-spines, stiff short spines terminating in 2 or 3 sharp deflexed points. They are large in proportion to the size of the flower, and are either closely appressed together or widely separated. The large-fruited ones, with nucules ¼ inch across, and large flowers, like *C. officinale* and *C. montanum*, are characteristic of Europe and North Asia, while the small-flowered ones, with small nucules, are most common in the tropics. The plants all inhabit open country, downs, and such spots. *C. officinale* and *C. montanum*, abundant in such localities in England, are greatly associated with rabbits. It is very common to find them at the mouth of rabbit burrows, where the animals, before diving into their holes, sit and clean their fur from any burrs which may have become attached during their rambles. The white horehound, nettles, and the hill-side forget-me-nots, with adhesive calyces, are likewise to be found in these spots. The loose earth thrown out by the rabbit forms a suitable growing spot for the hound's-tongue, and the animal can hardly run from its burrow in the fruiting season without carrying off some of the nucules. Sheep also carry these fruits about, and disperse them, as Beauverd records (in *Bull. Boiss.*, 1902, 1028), where he shows that they disseminate the plant. I have also found *C. montanum* growing against the walls of the ruined chapel on Lihou Island, Guernsey, where sheep had been constantly resting. *C. pictum*, which has rather larger fruits, in which apparently the nucules do not spread widely apart as they do in *C. officinale*, occurs from Morocco to Asia Minor, and from Portugal to the Caucasus, and is found in the Canaries, Madeira, and the Azores. Species allied to this are found from Siberia to Japan, and one large-fruited species, *C. molle*, grows in Chile, where it seems likely the viscachas disperse it, as the English rabbits do *C. officinale* and *C. montanum*. Of the small-fruited kinds represented by *C. fuscatum* and *C. micranthum*, absent from Europe and Siberia, there are numerous species or forms occurring in Africa, Madagascar, India, Siam, Cambodia, China, Sumatra, Java, Celebes, the Philippines and Australia. The panicles and racemes are longer and more slender, and widely spreading. The adhesive nucules are small enough to be carried about by small birds, but human clothing to some extent helps, and it is probable that in some places, e.g., Bourbon, their occurrence is entirely due to human agency; and though in the localities, in Java and Sumatra, where I have gathered these plants, the attachment to human clothing seemed to be the most probable cause of their present distribution, it is clear that the species are indigenous, and were probably carried there originally when wild animals were abundant.

Allied to *Cynoglossum* is the genus *Echinospermum*, in which the nucules are smaller than those of the small-fruited *Cynoglossum*, but similarly armed. They are found in South-Eastern Europe and Asia Minor, to Kamschatka, China, and India. One species occurs in Australia (*E. concavum*), possibly

introduced, and there are several species in North America. One species, *E. lappula*, common in Europe, has been met with in the Argentine and South Africa, and even in England on shingle in Sussex, and at Deal, and in Herefordshire, where it is believed to have been introduced in flax or grain. It is, however, also dispersed by the adhesion of its nucules to sheep. The absence of the genus from islands suggests that these plants are not often carried by birds, but probably by mammals, and certainly to some extent by domestic cattle. B. E. Read (in *Pharmaceutical Journ.*, 1925, p. 372), writing of Inner Mongolia, says :—" A pretty Forget-me-not (*Echinospermum anisacanthum*) is often seen. " Its prickly quadruple nuts stick to the back of animals, and are carried " hundreds of miles." Heinitz (in " On Epizoisk frospridning ") says that in North Sweden and Norway, *E. deflexum* inhabits the upper part of the pine woods where mammals are scarce, and the plant is dispersed by its nucules adhering to birds of prey—*Aquila* (Eagle), *Archibuteo* (Buzzard), *Bubo* (Owl) and Falcon.

Solanum rostratum (*Solanaceae*), the Buffalo-Burr.—This annual spiny *Solanum* is a native of North America. It is said to have been introduced into Australia from America in packing material, and its seeds in seed-wheat. Its fruits are small, round, and spiny, and in America it is doubtless spread by the American bison, as it is commonly found by their wallows. In Australia the fruits often become attached to the fur of passing animals. It is also dispersed as a tumble-weed (Maiden, in *Agric. Gaz.*, *N.S.W.*, 1904, p. 541).

Pedaliaceae.—This order of plants comprises a number of herbs, natives of America and subtropical Africa, erect or prostrate, which are remarkable for the fact that almost every species is adapted for the dispersal of its seeds by the attachment of the fruits to large mammals, and, further, that in the extraordinarily modified fruits, in some cases it is the stylar portion which forms the adhesive mechanism, while in others it is the evoluted wings of the body of the fruit which so functions, and in still other species the body of the fruit is armed with adhesive spines or hooks.

Apparently the most primitive genus in the order is that of *Sesamum*, one species of which has been widely dispersed by man for the use of its oily seeds. In this plant the capsule is cylindric, opening at the tip into 2 valves, the tips of which are acute. These 2 tips of the 2-celled fruit, which are developed from the bifid style, are lengthened in *Ceratotheca* into long points. From this we get the remarkable fruit of *Proboscidea* of North and South America, the " Mule-grab " of Texas, of which genus there are 4 species known. The pods are woody, about 3 inches long, fusiform, ending in 2 long curved sharp claws, hooked at the tip and 6 inches in length. In *P. altheaefolia* and *P. lutea* the body of the fruit is covered with short sharp spines. In *P. fragrans*, of Texas, and *P. peruviana* the spines are confined to the middle line. They add to the adhesiveness of the fruit to the foot of the animal by which they are transported. The seeds escape through a slit of dehiscence on the under side of the fruit (Pl. XX, fig. 4).

P. fragrans was accidentally introduced into South Africa during the Boer War, the seeds being brought in mule-forage, and I am indebted to Mr. Burtt-Davy for an account of the plant there. He says :—The fruit, fusiform in shape, like a boy's tipcat, lies on the ground, the long horns pointing upwards. When a mule steps on it, the fruit curves upwards, so that the long sharp horns clasp the fetlock of the animal, and, being springy and sharply-pointed, hold firmly to it. The curved processes on the body of the fruit, pointing towards the horns, cause the fruit to ascend the leg when the animal walks, and when it dehisces between the horns, the seeds are gradually dropped out of the capsule. The fruits also cling to the tails of horses and mules as they brush against them. The plant is clearly modified for dispersal by large ungulates, and though the

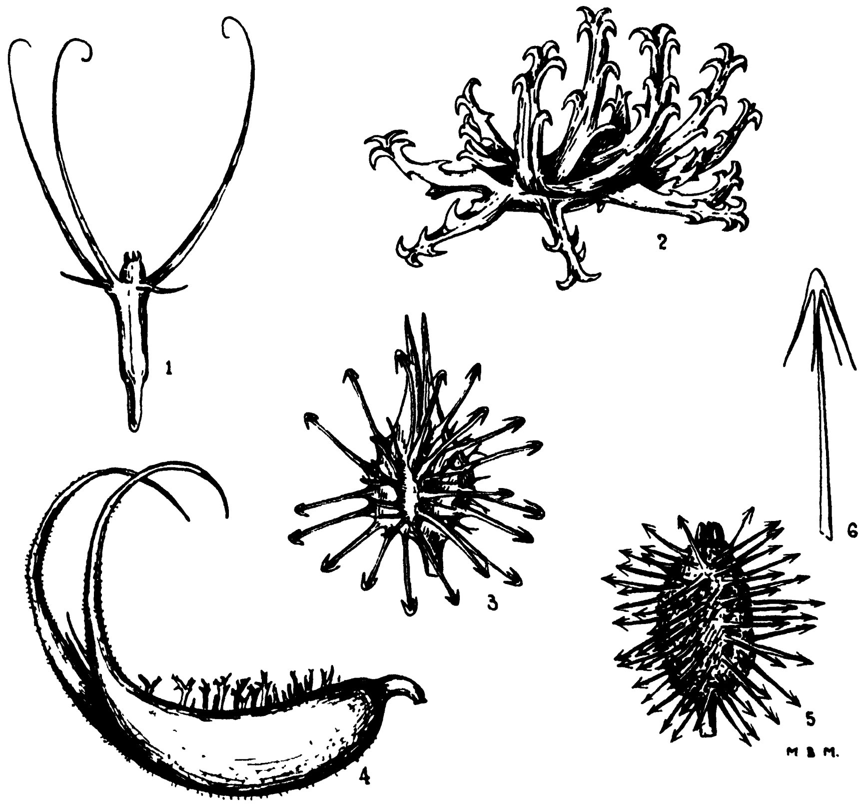
modern horse is a recent introduction into America, we know that in Tertiary times there were allied species, besides other ungulates, which could carry about this fruit on their legs, while deer, which could easily disseminate it, are still abundant in the Argentine and parts of America.

Martynia annua (*M. diandra*).—This ornamental herb with showy flowers is probably a native of Mexico and Brazil, but was introduced into the West Indies, San Domingo, as early as 1824. It was brought to India before 1843, and has naturalised itself there, and in Ceylon, Siam (1809), Mauritius (1864), and Madagascar (1879). In most of these places it is said to occur in rubbish heaps and in waste ground, but in India it seems to be widely spread. The fruit is woody, oval-flattened, and about 1 inch long, with 2 strong, sharp hooks at the top (corresponding to the horns of *Proboscidea* fruit) by which it is readily attached to fur of passing animals. In a newspaper of about 1876 Mr. Alfred Smee writes that in one of the hunting expeditions of the Prince of Wales (the late King Edward VII), in 1879, near Baroda, "a panther "was shot, and numerous 'seeds' (fruits) were attached to its skin. As the "panther moved about, it collected these, and when it rubbed, of necessity, against "the shrubs, it brushed them off." Mr. Smee obtained the seeds (or rather, fruits; he describes them as having 2 perfect hooks) and cultivated them, and they produced plants of the *Martynia*. The sharp hooks doubtless penetrated the skin of the animal. There can be no doubt that this plant owes its spread in India and Ceylon, where it appears to be common, to attachment of the fruits to such wild beasts. The absence of these animals in Madagascar, Mauritius, and Siam is doubtless the cause of its limited distribution there (Pl. XIX, figs. 20 and 21).

In another set of *Pedaliaceae* the evolution of the adhesive mechanism is on totally different lines. It is a modification of the angles of the fruit drawn out into wings. In *Holubia* the fruit has 4 simple wings from the angles; in *Pterodiscus* the fruit is a rounded 3-winged samara. These are, of course, wind-dispersed. In *Harpagophytum*, however, a native of South Africa, like the last two genera mentioned, these wings are modified into very powerfully adhesive organs. Two species are known. *H. Peglerae* has a fruit 2 inches long, fringed longitudinally, having 4 sub-foliaceous wings with flat spiny processes, not hooked, except 1 or 2 on the tip of the fruit. The 4 wings are on the side of the fruit, the upper surface of which, between the 2 pairs, is flattened, and armed with 2 short hooks in the centre, which, from herbarium specimens, appear to be viscid or resinous at the tips. The fruits, lying flat on the ground, could easily be picked up by the central hooks catching in the feet of an animal. From this form, by exaggerating the side-wings and cutting them deeply into broad linear wings armed with strong hooks, we can readily see how the form of the extraordinary fruit of *H. procumbens* was evolved. The plant lies flat on the ground, and the rather woody fruit is flat, about 3½ inches long and as wide. Its wings are cut into 10 or 12 linear, stiff, broad arms over 1 inch long, with strong hooks ¼ inch long, borne chiefly on the tips of these arms. The body of the fruit is about 1 inch across, and contains many seeds. The fruit, with numerous powerful claws, would easily become attached to the tail or feet or any part of an animal with which it came in contact, and would be very difficult to get rid of. It is said that a lion has been found starved to death from one of these fruits having become attached so firmly to its mouth that it quite closed it. It is probable that, having stepped on one of these fruits lying on the ground, it attempted to remove it from its paw by the aid of its mouth, and the fruit became so firmly attached to its lips that it could not open its mouth or detach the fruit (Pl. XX, fig. 2).

Uncarina peltatum, of Madagascar, is a half-shrubby plant with an oblong rounded, not flattened, capsule, 2 inches long and 1½ inches wide, with 4 low

PLATE XX.



ADHESIVE FRUITS.

FIG. 1.—*Trapella sinensis* (fruit, enlarged).
" 2.—*Harpagophytum prostratum* (fruit, reduced).
" 3.—*Uncarina peltatum* (fruit).
" 4.—*Proboscidea fragrans* (fruit, reduced).
" 5.—*Acaena millefolia* (fruit, enlarged).
" 6.— " " (a single barb).

[*To face p.* 596.

wings or ridges armed with a number of slender processes about 1 inch long, terminated with 4-winged knobs, the whole process forming a kind of club. The whole fruit, including the club, is thickly covered with glandular hairs, and must be readily adhesive to a passing animal. In a specimen of what appears to be another and undescribed species, the capsule is not covered with viscid hairs, but some of the clubs have 1 or 2 deflexed points or hooks. These fruits must readily adhere to the skin and hair of any passing animals (Pl. XX, fig. 3).

Pedalium murex.—This herb occurs in tropical Africa, South India, and Ceylon. It is a habitant of sandy shores, expecially near the sea, and is found in Socotra and Madagascar also. The fruit is $\frac{1}{2}$ to $\frac{3}{4}$ inch long, narrowed below into a short thick stalk, ovoid, 4-angled, armed with a sharp point and 5 sharp horizontal spines from the angles. Like the fruits of *Tribulus*, it causes wounds to the feet of natives and animals, and undoubtedly may be conveyed from one place to another by attachment to animals' feet, though I would suggest that the spines were primarily developed for anchoring the fruit to the sand. In fact, its history is much like that of *Tribulus* and *Neurada* (Pl. XIX, fig. 24).

Somewhat similar in action may be the spines which cover the capsules of *Josephinia*, in one species of which the capsules are $\frac{1}{4}$ inch long and covered with spines. This is distinctly an island plant, found in Lombok, Letti, Nioa, and Timor Laut, as is *J. grandiflora*, of Australia, with more slender spines, which seems to be mainly an insular plant, and is recorded from Lizard Island, Three Isles, and Low Island, off the Australian coast. *J. eugeniae*, of the inland of Australia, appears to have viscid fruits.

Rogeria adenophylla, a native of Northern Africa, has a conic fruit tapering to a point, $1\frac{1}{2}$ inches long. It dehisces at the top, and on the broad base are 5 or 6 short deflexed spines, often, but not always, hooked. In R. *longiflora* the oblong conic fruits, $1\frac{3}{4}$ inch long, are usually quite unarmed, except that the sepals become hard and transformed into minute hooks; but some fruits have short conic processes at the base, on the median line of the carpel, sometimes as much as $\frac{1}{4}$ inch long, but straight and not hooked. It is hard to see how these conic processes can be of any value as adhesive organs, but they seem to be the preliminary structures evolved into decurved hooks in R. *adenophylla*.

Pretrea zanguebarica is a native of South-East Africa, where it grows on river banks, borders of lakes, and sandy places by the sea. Its fruit consists of a thick round disc, from the centre of which project 2 short, sharp, conic spikes, clearly corresponding to the 2 claws of *Martynia*. The disc appears to be derived from a receptable at the base of the ovary. As it seems to be associated with rivers and lakes, and is recorded from the mouth of the Zambesi River, and on Mafia Island, Zanzibar, I conclude it is dispersed to some extent by water. It is described as a troublesome weed, and Monteiro says, "The "seed vessel is a diabolical botanical invention with 2 hard sharp spikes," and Miss Alice Pegler says, "It injures animals' feet and bicycle tyres," so that it is probably disseminated in much the same way as *Tribulus*. The fruit does not dehisce, and contains only 1 or 2 seeds (Pl. XIX, fig. 12).

Trapella.—This extraordinary Chinese and Japanese plant is usually referred to the *Pedaliaceae*. It is an aquatic plant occurring in lakes, and having foliage somewhat resembling that of *Trapa*. The flowers are solitary, and the fruits are borne on rather long axillary pedicels. They are cylindric and about $\frac{1}{4}$ to $\frac{3}{4}$ inch long, 1-seeded, and inferior. After the fall of the corolla, the calyx-lobes close over the top, and there develop 5 spines just below them and at the top of the fruit. Two of these spines are short, and project at right angles to the fruit; the other 3 are $1\frac{1}{2}$ to $1\frac{3}{4}$ inch long. These 3 are slender, curved,

and hooked at the tip. It is difficult to see how these can correspond to the carpellary claws of *Proboscidea*, but they probably function as aids to dispersion. It has been suggested that they may be dispersed by adhesion to fish, as, when ripe, they float under, or on the top of, the water; but it is more probable that they adhere to ducks, as has also been suggested. The pool in which the plant was found was one of a number, the rest of which did not contain it, but there does not seem to have been any stream connection with the pool by which fish could have come. Could batrachians, which wander from one pool to another, have been the carriers?

The plant was first described by Prof. Oliver, and figured in Icones Plantarum, 1595, and fully described and figured by F. W. Oliver, *Ann. Bot.*, ii, 75 (Pl. XX, fig. 1).

Microtea (*Phytolaccaceae*).—Small weak weeds of Africa, West Indies, and South America, with very small fruits $\frac{1}{8}$ inch long. In many of these the fruit is covered with short papillae, prolonged in *M. glochidiata* into short hooked processes. These plants are inhabitants of open ground, paths, etc., all over South America. Such small fruits could readily be dispersed by adhesion to rats or any small mammals.

Zippelia lappacea (*Piperaceae*).—A herb about 1 foot tall, with a terminal spike of globose fruits armed with hooked spines. This is found in forests, rather locally, in the Malay Peninsula, Java, and Sumatra. The spikes of fruit are borne opposite a leaf, and are lax, the fruits being rather distant. The fruits, like those of a pepper, are 1-seeded. It is probably dispersed by attachment to fur of passing animals, such as the Mouse Deer (*Tragulus*), or wild pigs.

Adhesion of Seeds by Hooked Hairs.

Seeds provided with hooked bristles or spines for attachment to, and transport by, animals are by no means common. A curious instance occurred in the jungle water-lilies of the Malay region (*Barclaya*). These plants occur in shallow streams, usually only 6 inches deep, in the dense forest of the Malay Peninsula and Borneo. The soft capsules readily dehisce, and emit a number of very small elliptic or globose seeds covered with short curved processes. These readily adhere to the hair of wild pigs, which inhabit these forests, and which form mud-wallows in damp spots. I have found fine plants of *B. Motleyana* in a pig-wallow in the Tahan Forests, quite unconnected with any streamlet, nor did I see any other plants anywhere near this wallow (Pl. XIX, fig. 23).

Adhesion of Bulbils.

Remusatia vivipara (*Araceae*).—This remarkable Aroid appears to flower and fruit very rarely. It is mainly propagated by bulbils. These are borne in tufts on erect simple branches on the rhizome (turions). They are small, red, about $\frac{1}{4}$ inch long, very numerous, with many bracts ending in slender terete hooked points. These bracts are very adhesive to cattle, and there can be little doubt that the plant is mainly disseminated in this way (Pl. XIX, fig. 22).

It is fairly abundant in the Himalayas, and is found in Tavoy, Yunnan, Siam, Ceylon, Java, and has been met with in Christmas Island, where it has only been found in one spot, once, by Andrews. I failed to see any trace of it, as the original locality was covered with a vast mass of debris from the phosphate quarries. Its occurrence there must be due to its bulbils having been brought attached to birds, no doubt, from Java, its nearest locality.

Another species, *R. Hookeriana*, and one of the genus *Gonatanthus* (*G. sarmentosus*), occur in India and Siam, and are reproduced by bulbils quite similar, except that the points of the bracts are thin, weak, and not hooked. These are evidently wind-dispersed, and are less widely distributed.

Plants Dispersed by Adhesion to the Wool of Sheep.

While the fruits and seeds of many plants are readily attached to the hair of cattle, horses, antelopes, etc., a much more attractive coat to burrs and adhesive fruits and seeds generally is to be found in the long, curly, dense wool of the sheep. It is not to be wondered at, therefore, that very numerous plants owe to these animals their present distribution all over the sheep-lands in the northern and southern hemispheres. Sheep not only collect burrs by browsing on low vegetation, but also by lying down among it at night, or resting against bushes. The wool is greasy, and thus collects, not only fruits with hooked bristles and the long awned spikelets of many grasses, but also viscid seeds, and even smooth or shortly hairy fruits. Flocks are moved from one place to another, often many miles apart, and have also been carried from Europe to North and South America, distant parts of Africa, and the north temperate regions of Siberia and India, and to Australia and New Zealand. They have carried with them in their fleeces seeds and fruits of innumerable plants, and in this way European plants have been borne to North America, to the Argentine, to South Africa and to Australasia. When the South African sheep were carried to Australia, they bore with them many African plants. Later, wool was sent from the Colonies and other countries to Europe, which carried similar burrs from these distant lands, and these have now become established in Europe. In some cases, e.g., the Medicks (*Medicago*), the burrs have been transported to the Argentine and Australia from their habitats in Europe, have grown abundantly, and formed sheep pastures, and have been carried back again in the wool exported to Europe, and become established in new localities there.

Two important accounts of plants which have appeared in Europe at the spots where colonial wool was washed are "The Adventive Flora of the "Tweedside," by Miss I. M. Hayward and G. C. Druce, and the "Flore Adventive de Montpellier," by Thellung.

The former of these two works gives an account of the alien plants round the wool-washing works at Galashiels, and includes plants from all parts of the world's sheep-producing area. In the latter the wool seems mostly to have been derived from the Mediterranean region, and to have brought plants from the Mediterranean and Asia Minor. Both lists give all kinds of alien plants found in their districts, but as many of these appear to have come in ballast, or in other ways unconnected with sheep, I have only extracted those which are definitely associated with wool-waste and wool mills.

The origin of the Sheep (*Ovis aries*) is wrapped in some obscurity, and it is possible that the animal is descended from some species which has now disappeared. There are a number of species of *Ovis*, but none seems likely to be the originators of the domestic sheep. There can, however, be little doubt that it originated in Asia. It was entirely absent from Europe in Palaeolithic times, and appears first in the Bronze Age; and as the domestic fowl (which must have been originally derived from India) appears with it, it may be suspected that both came into Europe with an Asiatic race of men. A previous wave of immigrants, doubtless from the East, had brought the flax and wheat, and with them came some of the common weeds of our cornfields, and it is probable many of the European burr-weeds came about that time in the fleeces of the sheep. The sheep soon spread over Europe, and thence to America. Miss Hayward states that the wool mills on the Tweed, started in 1581, were supplied only with wool from the neighbourhood till 1774. In 1788 Capt. Phillips took 29 sheep from England to Australia, and in 1840 Australian wool began to come into England. German lamb's wool was introduced into England in 1840.

List of Plants Distinctly Associated with the Wool of Sheep.

RANUNCULACEAE.

Ranunculus arvensis, achenes spiny (Hayward), R. *trilobus* (R. *sardous*), achenes smooth. Both these plants were in Britain in the Interglacial period. R. *muricatus*, spiny, a Mediterranean species now in America, Juan Fernandez (1873), Australia, New Zealand. May have come in Chilian wool.

PAPAVERACEAE.

Papaver hybridum.—The bristly capsules of this, as well as those of *P. argemone*, become entangled in wool (Hayward). The latter species first appears in Britain in Roman times. No other red poppy known to occur as early.

Argemone mexicana, a native of Central America. Now occurs in Africa, Asia, Australia, in Cochin China (Loureiro, 1790), (Hayward).

CRUCIFERAE.

Nasturtium nanum, of South America. Tweedside Mills (Hayward). *Sisymbrium Turczanowii*, native of South Africa. Fruit entangled in the fleece by its bristly covering. Tweedside (Hayward). *Sisymbrium brachycarpon*, of North America, and *S.* sp., allied to *S. myriophyllum* of Ecuador, near wool mills, Scotland (Hayward); *S. runcinatum*, Montpellier (Thellung).

Lepidium perfoliatum, native of Asia Minor. Montpellier (Thellung), *Lepidium* sp., Miss Hayward records as occurring on wool-wash heaps, 5 species from South Africa, 1 from North America, 3 from South America, 4 from Australia, and 3 of unknown origin. Of *L. papillosum* she writes:— "Seeds exude abundance of clear viscid mucilage." *L. sativum* and other species are known to possess viscid seeds also, and this, doubtless, plays an important part in the dissemination of the genus.

Muricaria prostrata, an Algerian *Crucifer*, is recorded by Thellung as occurring in wool at Montpellier. It is a low herb with small hairy elliptic pods, 1-seeded and armed with 4 tubercles, 2 of which are acute. It would be readily caught in the wool.

Clypeola cyclodontia.—This plant was first discovered in wool-washing ground in Montpellier by Thellung. It was later found in Algiers. The genus is one of low herbs, possessing flat, disc-like, 1-seeded pods. In some species the pods are quite glabrous. In *C. jonthlaspi* some forms are perfectly glabrous, others pubescent, and some roughly hairy. These round thin pods, ¼ inch wide, with a central seed surrounded by a wing, are destined to be dispersed by wind. In the desert species the whole plant is more or less hairy. In *C. cyclodontia* the edge of the wing is cut into about 18 broad truncate lobes, and the whole fruit covered with stiff hairs. It is easy to see how the wool of a sheep would pick up these fruits.

MALVACEAE.

Malva nicaeensis and *M. pusilla* have been found by Miss Hayward in wool-washing grounds.

CARYOPHYLLACEAE.

Silene gallica.—Miss Haywood notes: "Abundant in California, and "doubtless conveyed to a height of 2,800 metres in Bolivia and Chile. The "viscid inflorescence easily adheres to animals, and thus the plant rapidly

"extends its area." This little plant certainly occurs commonly in sheep pastures and downs in England.

GERANIACEAE.

Erodium botrys is a Mediterranean plant now occurring in the Canaries, Madeira, America, and Australia. "The corkscrew-like awn has 6 or 7 turns, "whereby it readily penetrates the fleece" (Hayward). *E. cicutarium* of Europe, *E. cygnorum* of Australia, *E. chium* and *E. romanum* of South Europe, are mentioned also by Miss Hayward, and *E. laciniatum* by Thellung as occurring in wool mill waste heaps. Probably most of these storks-bills are carried about by flocks, and *E. cicutarium* is said to be dispersed largely by cattle also.

Monsonia brevi-rostrata, of South Africa, occurs on Tweedside (Hayward). This herb appears to be rare even in South Africa. It grows in open fields, and has a fruit like that of *Erodium*, with a beak 1½ inches long.

HYPERICACEAE.

Hypericum crispum occurs on wool heaps (Thellung).

CISTACEAE.

Helianthemum Lippii.—Montpellier. Some of the species have viscid seeds (Thellung).

ZYGOPHYLLACEAE.

Tribulus terrestris is stated by Burtt-Davy to adhere to sheep's wool in South Africa. It is a well-known adhesive fruit.

LEGUMINOSAE.

Medicago.—A large number of the Medicks have been transported from one place to another by their adhesive fruits being attached to sheep. *M. denticulata*.—Fruits frequently found in Argentine wool (Hayward). This is a European plant, which has been carried by sheep to America and most sheep-breeding lands, and brought back in the fleeces to Tweedside and other wool-cleaning spots. *M. arabica* (*M. maculata*) and *M. minima* and *M. laciniata*, from Mediterranean Africa, come up in gardens dressed with wool waste. It seems likely that these Medicks originally evolved in the area from Asia Minor to Persia, and have travelled in the sheep's wool to Europe. In wool sent me by Mr. Perrott from Dera Ismail Khan, North India, I found fruit of *M. minima*. *Melilotus sulcata*, a Mediterranean plant ranging to Palestine and the Canaries, has appeared from wool waste. *Trifolium subterraneum* and *T. arvense* have appeared in wool, as well as *Trigonella polycerata*, of Spain. *Scorpiurus subvillosus* is an alien in England brought in wool (Dunn).

Astragalus epiglottis is a dwarf plant of the Mediterranean region, chiefly from the African side. The 1-seeded pods are small, flat, and hairy, triangular, with a hooked stigma. The fruits would certainly become entangled in the fleeces of sheep lying on this plant. It has been found at Montpellier in wool waste by Thellung, together with *A. cruciata*, a taller plant with a hairy pod and hooked stigma. *Hippocrepis bicontorta*, a native of Algeria with an extraordinary pod bent into a semicircle, and eventually perforated so that the holes between each segment form two long sharp points to each, is found at Montpellier by Thellung.

ROSACEAE.

Acaena anserinifolia from Australia, and *A. ascendens* from New Zealand and Patagonia, have appeared at Tweedside (Hayward), and *A. sanguisorbae* has lately been found on Hey Tor, Dartmoor. How it got there is quite obscure, but it is often cultivated on rockeries, and may have been transported by the adhesion of its fruits to the wool of sheep and rabbits, or human clothes. The dispersal of these very adhesive fruits is mentioned under Adhesive Fruits, p. 588.

CRASSULACEAE.

Tillaea Vaillantii, of South Europe and Africa, *T. pharnaceoides*, of Persia, India and Africa, *T. Sieberiana*, of Australia, occurred at Tweedside, doubtless introduced in wool (Hayward). The minute seeds of these plants might adhere to a fleece.

UMBELLIFERAE.

Eryngium triquetrum, of Asia Minor and Morocco, at Montpellier (Thellung). It has small obconic fruits with 5 erect short stout spines.

Daucus glochidiatus, of Australia and New Zealand.—Fruits found in wool (Hayward), and *D. sahariensis*, of Algeria, plants found at Montpellier (Thellung).

RUBIACEAE.

Galium aparine.—This is largely transported by sheep. Miss Hayward records its fruit being carried in their wool.

COMPOSITAE.

A large number of these plants are dispersed by sheep, as the achenes are often hairy, and the sepals form spines which penetrate the fleece, and remain attached until the locks of wool are shed or the fleece shorn off. The Burdock (*Arctium Lappa*) is commonly disseminated by sheep. *Xanthium strumarium*, *X. spinosum*, and *X. ambrosioides* are so dispersed, the latter from the Argentine. *X. spinosum* is said to have been introduced into South Africa in the wool of the Merino sheep (Shaw, *Journ. Linn. Soc.*, xiv, 202).

Brachycome collina, from Australia, has achenes bordered by a wing divided into linear lobes hooked at the tips. As Thellung remarks: "The fringed "wings of the fruit afford a ready way for its adherence to the wool, and the "occurrence of the plant in the bed of the River Orb, near Montpellier, is "attributed to the adjacent wool-washing."

Calotis cuneifolia, a native of Australia and New Zealand.—This herb has flat obovate achenes, with a pappus of 3 rigid barbed bristles, and 2 broad membranous truncate scales. Fruiting heads form a ball 3 to 4 lines in diameter ($\frac{1}{4}$ to $\frac{1}{3}$ inch). It has been found in wool waste on the Tweedside and in Yorkshire. It infests sheep pastures in many parts of Australia and New Zealand. The achenes cling by the barbed bristles to the sheep's wool and become inextricably entangled, and so imported with the wool (Hayward). Maiden says it is a source of great irritation both to man and domestic animals. *C. hispidula* has also bristly fruits, which are often present in great quantities, especially in Sydney wool, so that portions of the staple are quite matted with them (Hayward, who gives a good figure (22) of these fruits).

Helianthus sp., *Carduus* sp., *Centaurea melitensis* and *C. nicaeensis* (Thellung), *Millotia* sp. and *Bidens pilosa*, *Soliva* (2 species from South America), *Isoetopsis* from Australia (Hayward), *Pulicaria laciniata* of Algiers, *Anthemis mixta* var. *aurea*, and 6 kinds of *Artemisia*, are recorded as introduced in wool, by Thellung. The Wormwoods (*Artemisia*) are recorded to have viscid flower-heads and achenes in many species. *Gnaphalium luteo-album.*—Of this, Miss Hayward writes :—" Doubtless it is from Australian or Cape wool that it has come to " Tweedside." This plant is extremely widely distributed, and turns up in unexpected places. Its fruits may be to some extent dispersed by wind, and by adhesion to birds, but I cannot definitely account for its appearance in many localities.

Cryptostemma calendulaceum, of South Africa, was introduced into Australia in 1850, and thence to New Zealand. It appears at Tweedside, and has also been found in Portugal and Spain. The achenes are very small, and completely covered with thick wool. *Cassinia arcuata* is stated by Ewart to be disseminated in Australia in sheep's wool, and also by wind.

Dicoma tomentosa is a weedy plant of Africa and India, in which the outer bracts on the involucre are spine-like and barbed. I found a head of this plant in the sheep's wool sent to me from Dera Ismail Khan, North India, by Mr. Perrott.

A number of *Compositae* with plumose pappus are disseminated by sheep. Hayward gives *Erecthites* 3 species Australian, *Senecio*, 4 species Australian, 4 South African, 1 Egyptian, and 1 Brazilian. The achenes of *Hypochaeris glabra* frequently occur in Australian wool. It is of European origin, and has been accidentally introduced, perhaps in sheep's wool, to Australia, and afterwards comes back by the same means to Europe. Thellung adds *Picris echioides* (*Helminthia*) and *P. hieracioides*, also transported by sheep in Australia (Ewart), and *Crepis foetida* var. *glandulosa*. In some of these the achene is sticky, and some have processes on the achene, but the probability is that the wetted pappus adheres to the wool. Some *Compositae* possess viscid mucilaginous achenes, as in *Cotula*, of which 8 species were found in Tweedside, they are natives of the southern hemisphere; and the little *Centipeda orbicularis* probably came in the same way.

POLEMONIACEAE.

Gilia squarrosa is said to be dispersed in South America by its viscid seeds adhering to sheep's wool.

PLANTAGINEAE.

Plantago virginica, of North America, and *P. varia*, of Australia, both appeared on Tweedside; doubtless their viscid seeds had adhered to sheep's wool.

BORAGINEAE.

Echinospermum Lappula and *Eritrichium australasicum* have been found at Tweedside by Miss Hayward. They are well known as sheep-dispersed plants, as is *Cynoglossum montanum*, which I have found in Guernsey in places where sheep had been lying. Thellung adds *Rochelia disperma* and *Echium maritimum*, and Clarke (" Farm Weeds of Canada ") gives also *Echium vulgare* nutlets found frequently in wool, and probably many more of the adhesive-fruited *Boragineae* are so dispersed.

SOLANACEAE.

Datura stramonium and *D. tatula* :—Of these plants, seeds have been found in sheep's wool by Miss Hayward, and this is perhaps one method by which these plants are dispersed throughout the world, although they have no adhesive apparatus. Thellung mentions *Physalis viscosa*, of South America, and *Solanum juvenale* as occurring in wool-washings at Montpellier. *S. rostratum*, with spiny fruits, is doubtless dispersed also by wool.

VERBENACEAE.

These are represented by *Verbena supina*, found by Thellung at Montpellier, and probably the adhesive fruits of the roadside *V. officinalis* are similarly dispersed.

LABIATAE.

The seeds of *Lamium* sp., from Australia, and *Marrubium vulgare* have also been found in wool at Tweedside.

AMARANTACEAE.

Mr. Perrott, of the Indian Police, kindly sent me a bag of sheep's and goats' wool from Dera Ismail Khan, North West Provinces of India, containing burrs which had been picked up by the sheep in their wanderings. I examined the wool, and found a considerable number of burrs of different species of plants. Among them the most abundant was *Aerua scandens*, which is supposed to be a lofty climber, but the district from which these burrs came is not forested, but rather desert. The little fruits are 2 mm. long, the base of the perianth covered with dense woolly hairs, the sepals being lanceolate and papery. These tiny fruits were deeply and firmly fixed in the wool, which seemed to curl round them.

The plant is abundant in Northern India, and also in the south, in Madras. Gamble described it as an undershrub, climbing on bushes. The flowers are very numerous, in dense spikes. It is rather curious that a fruit provided with silky hairs only should so work its way into the fleece. The *Aeruas* are very widely spread over dry regions in Africa, and *Ae. scandens* in India, Burma, Cambodia, Siam, Philippines, Madagascar, Timor and Timor Laut. In these outlying areas, no doubt, the plant has been introduced in sheep's or goats' wool. I observed that several fruits among those sent from Dera Ismail Khan were still carrying good seed.

Most of the species are readily dispersed by wind, as the fruits are very light and plumed (Pl. XVII, fig. 16).

The next most abundant burr was the fruit of *Pupalia lappacea*. In the flower-head of this plant the outer flowers are usually reduced to bristles armed with short hooks, by which they are readily attached, and 2 or 3 of these flower-heads were found in the wool, but the fruits were more frequently found there. These are oblong, about ¼ inch long, tough utricles, woolly, and armed with numerous stiff hooked spines, usually in threes. These are the most persistently adhesive burrs I know, clinging tightly, not only to cloth and wool, but very firmly to the fingers. The plant is a straggling herb about 1 foot or more tall, with a spike of these burrs somewhat distant from each other. Apparently the leaves are a favourite food of goats, as a collector in Kew Herbarium writes that in Northern India it usually grows in bushes,

where the goats cannot get at it. It is found all over Africa and India, Ceylon, and as far north as Persia (Pl. XVII, figs. 13 and 14).

CHENOPODIACEAE.

These herbs are very largely dispersed by sheep, a great variety of the species and varieties occurring on wool waste ground at the Tweedside. Among them is specially noteworthy *Chenopodium auricomeforme*, probably of Australian origin, but only known from wool heaps, first at a wool-combing factory in Switzerland, and later in a wool rubbish heap on Tweedside.

POLYGONACEAE.

Two species of Australian Docks, *Rumex* from New Zealand and R. *nepalensis* from India, have appeared at Tweedside, and Mr. Maurice Horner sent me some New Zealand wool containing fruits of *Rumex conglomeratus*, which had long been introduced into New Zealand.

URTICACEAE.

Pilea microphylla, of South America, appeared at Tweedside, evidently brought in sheep's wool.

MONOCOTYLEDONS.

Except for grasses, few *monocotyledons* appear to be carried about by sheep in their fleeces. *Juncus bufonius* var. *grandiflorus* from Chile, and a species allied to *J. uruguensis* from South America, both probably attached by seed-viscidity, and *Cyperus congestus* and a *Carex* appeared on skin heaps, or wool, at Tweedside (Hayward). Grasses are remarkably liable to be transported by sheep, and numbers were found both at Tweedside and Montpellier.

Eriochloa ramosa (*E. acrotricha*), of Africa and Australia, *Tragus racemosus*, *Aristida angustata*, of South Africa, *Nasella* (2 species), from the Argentine and Bolivia, *Themeda triandra* (Montpellier, Thellung), a native of Africa, *Agrostis lachnantha*, of Abyssinia and the Cape, *Polypogon maritima*, *P. elongata*, *P. monspeliensis* and *P. linearis*, of Chile. (*P. monspeliensis* is said to adhere by its scabrid awns to wool and skins. This is, as are some of the other species, very widely distributed, and occurs on remote islets in some parts of the world where it is usually supposed to have been introduced by man, but this wool dispersal suggests that it may have been introduced by adherence to birds' down.) *Alopecurus* (2 species), *Apera* (*Agrostis*) *Spica-venti*, all occur on the Tweedside or by the wool heaps.

Of the genus *Stipa*, so well known from its spikelets penetrating into the skins and fleeces of animals, 9 species from South America were found on Tweedside, among which was *Stipa neesiana*, which has appeared in the vicinity of wool factories in Scotland, France, Italy and Germany, and a few years ago there was a large clump of this grass on the Mortlake rubbish dump in Surrey. In Argentine it is very troublesome when in fruit, as the sharp hard calli of the spikelets readily bore into the skin of animals, causing painful wounds (Hayward).

Prillieux (in an article " Sur les fruits de Stipa qui percent les peaux des " Moutons Russes ") records how he found in sheep imported from Russia to Villette, in France, abundance of fruits of a species of *Stipa*, apparently

S. capillata, penetrating the skins, and very injurious to the hands of persons handling the sheep or their skins.

R. Miller Christy (in "Notes on the Flora of Manitoba") records the damage done to sheep and woolly-haired dogs by *Stipa spartea*. The sharp spikelets of this grass, he thinks, were probably originally dispersed by the American bison, but, since that has now become almost extinct, it owes its present dispersal system to domestic animals. Sheep and dogs, passing through this grass, collect so many of these penetrating spikes that they are severely injured, and he records cases of animals, both lambs and dogs, having to be destroyed through injury by this grass.

Cenchrus tribuloides is more injurious to wool than anything else in North America, according to Lyster D. Dewey ("Migration of Weeds," *Year Book of Agriculture, U.S.A.*, 1896, p. 263). *C. australis* is described by A. M. Lea (*Trans. & Proc. Roy. Soc., South Australia*, xxxix, p. 92) as an insect-catching grass, as he found many insects, of various kinds and sizes, caught by it. He adds that the burrs of this grass often catch in the horses' tails and manes, as well as in the hair of dogs and wool of sheep. The grass has a long, slender, erect spike of about 80 spikelets, each of which is surrounded by a fringe of about 50 prickly hairs, and each hair is studded with short retrorse spines, at least 500 to a hair. This Australian species is therefore readily dispersed by mammals.

Cockayne points out that the grass *Danthonia* is regularly distributed over wide areas in New Zealand by the attachment of its hairy seed to the wool of sheep, and says that the purchase of sheep from country where *Danthonia* has seeded freely is regularly effected with the express intention of bringing in considerable amounts of seed in the fleeces to places where the grass is wanted, and does not occur. Four species of *Danthonia* from Australia and New Zealand were found by Miss Hayward on Tweedside.

Deyeuxia retrofracta, of Australia.—The pointed seeds of this grass are very injurious to wool, and cause blindness in sheep. *Avena fatua*, the Wild Oat.—Seeds extracted from Tasmanian wool were grown by Miss Hayward. This is a native of Europe, and must, in the first place, have been carried by sheep to Tasmania.

Chloris truncata, of Australia (Hayward), is found in the vicinity of wool sheds. This was possibly brought in the packing, as *Ch. barbata* certainly is carried about in this way. *Eleusine indica* (Hayward).—This may be one way in which this extremely abundant tropical grass is carried about, but it is certainly not the only way. I am very doubtful as to how it has travelled so widely.

Dissanthelium supinum, from Bolivia and Peru, occurs at Tweedside, and *Eragrostis*, 2 species, 1 in Tweedside and 1 in Montpellier, both African in origin.

Phalaris canariensis (usually carried about the world as bird seed), *Aira* sp., *Setaria* sp., *Molinia coerulea* (a common English marsh grass), *Festuca bromoides* and an *Andropogon*, of these, seeds were taken from wool, by Miss Hayward.

Hordeum murinum.—"The fruits have very long awns which work their "way into the fleece when the flock is feeding and lying down, and are "practically irremovable; any attempt in that direction merely aggravates the "trouble. The awns even penetrate into the skin. The seeds are mostly "found in Port Philip wool" (Hayward). Miss Hayward has grown plants from these seeds, and gives a good photograph showing skins pierced by fruits. The Wall Barley, so common in Europe, is also dispersed by attachment to the clothes of passers-by, and by wind and rain-wash. In Australia it is reported to cause injury to the eyes, teeth and throats of horses and cattle, as well as of sheep. In England it usually grows along roadsides, or by walls, and not in pastures where it could get into sheep's wool. *H. jubatum*.—

This grass is a serious enemy to West Canadian stockholders, a source of much injury to horses, cattle, and sheep. The barbed awns and seeds work into and penetrate the mouth and other parts of animals (Hayward). Maiden gives photographs of serious ulceration of the jaws of sheep caused by the awns of this plant. *H. violaceum*, a native of Asia Minor and Persia, and *H. muticum*, of the Argentine, also occurred on the wool-waste heaps at Tweedside.

Bromus sterilis, and the *Bromus arenarius*, of Australia, were also found there. Of *B. rubens*, L. D. Dewey (*Year Book of Agriculture, U.S.A.*, 1896, 263) writes thus :—" In some parts of Oregon the sheep tracks are lined with this " grass, the long barbs of which cling to sheep."

FILICES.

Pteris aquilina.—Branches of the bracken bearing spores are occasionally found in New Zealand wool (Hayward). This is interesting as showing how this fern may be dispersed. I have elsewhere mentioned how it was conveyed by spores on rice bags to the Pahang mountain plateau.

General Notes.

Holmboe (in " Studies of Cyprus ") states that he found fruits of *Medicago* and other *Leguminosae*, *Caucalis*, *Orlaya*, *Torilis*, *Daucus*, *Ranunculus*, *Erodium* and *Stipa* in the wool of sheep in Cyprus. The *Stipa* occurred chiefly on the abdomen through the animals lying down on it, but also on all other parts, and often on the thick tail. Sheep and goats often go 5 or 10 miles a day feeding on pastures. The fruits are loosened when the sheep pass through the Maquis copses. He observed that, when the sheep and donkeys roamed free, the seeds most readily adhere to the abdomen, sides, and breast, but here is the greatest chance of their being swept off by the bushes. Seeds affixed to head and manes, especially near the eyes, remain much longer attached, as the animals hold their heads up when passing through the bushes. When he bade the servant not to remove the fruits of *Medicago* and *Caucalis* from his donkeys' manes, they remained there for 2 or 3 weeks, undisturbed, though the animals passed through woods and coppices.

Cockayne calls attention to the minute size of some seeds, enabling them to remain in the fleeces of sheep : Foxglove (*Digitalis*) and Mullein (*Verbascum*) are good representatives of this class. The presence of Foxglove on a farm in New Zealand can often be traced to the bringing of stock from a Foxglove-infested country. The seeds of Foxglove and Mullein are not viscid, but such seeds may readily be attached to the greasy wool of the sheep lying down on ground where the seed has been sprinkled by the plants.

Both Miss Hayward and Thellung mention many more plants occurring round the wool-washing localities, which may probably have been introduced in the wool of the sheep, and may be classed as sheep-dispersed. Indeed, all the alien plants of the Tweedside whose original homes were in the Argentine and Bolivia, in South Africa, Australia and New Zealand, were almost certainly brought in sheep's fleeces. The Montpellier plants are mostly of Mediterranean origin, and some seem rather to have come to the warehouses in ballast or packing, or in grain. Their lists, however, give a very good idea of the great importance of the dispersal by sheep, especially during the last century. These animals very readily pick up the seeds and fruits as they travel, even minute seeds, as shown by Cockayne. Their wool is shed in locks, or torn off by vegetation, and the seeds germinate where they fall, or they are shorn, and their wool carried to distant countries, where, during the process of washing

and cleaning, the seeds become removed and, germinating, add the plants as aliens to the flora of that particular locality.

Before the introduction of the sheep in the Bronze Age, it is certain that their place as seed-dispersers was taken by the woolly mammoth and rhinoceros, deer, wild goats and wild sheep, horses, wild cattle and bison, in the north temperate regions, while the equally abundant ungulate fauna of America and Africa and the marsupialia of Australia preceded the modern flocks and herds, and were responsible for the primary evolution of adhesive fruits and seeds.

Wool is characteristic of the coats of animals of cold climates, so that it is from the northern and southern temperate or cold regions that most of these plants come. Extensive as these lists of plants which have migrated by the movements of domestic animals are, they could be greatly increased by research in India and tropical South America, as well as parts of Africa. It is clear that, besides plants specially adapted for adhesion to animals, many others may be accidentally adherent, especially to the greasy fleece of the almost ubiquitous sheep.

CHAPTER VIII

DISPERSAL BY ADHESION DUE TO VISCID EXUDATION

Viscid-glandular Bracts—Viscid Calyx—Viscid Fruits, Viscid Drupes or Berries, Adhesive Achenes—Viscid Seeds.

In a number of plants there is a viscid resinous or gummy exudation, usually from short-stalked glands, or hair-like processes, on the tip of which is a small gland. These stalked or sessile glands may occur in all parts of the plant (stems, leaves, bracts, calyx and fruit), and are especially characteristic of plants of dry regions. In plants in which this gummy exudation is destined for adherence to animals for the purpose of dissemination, it is usually confined to the calyx, fruit, or to the bracts, and the fruits are detached below the portion which bears the viscid glands.

Kerner points out that in some cases the unripe fruits or seeds are protected from the attacks of animals, when they are young, by this exudation of gum or resin. Such exudations also protect the young fruit from injury by rain and the attacks of fungi, in the same way that buds are often protected by resinous scale leaves.

Another origin for these viscid, resinous, or mucilaginous exudations is to be found in their use for the purpose of restricting excessive transpiration and desiccation, and for water storage. Warming (" Oecology of Plants ") states that mucilage absorbs water readily and parts with it slowly. It is for these reasons probably that we find a larger tendency to viscid exudations in deserts, dry open places, and seashores, than in damp, swampy districts or forests. It is by this exudation of gum or mucilage that we get another form of disseminating apparatus. The most common form of attachment by viscidity is that of the fruits enclosed in the calyx-tube, which is adnate to them ; but there are also examples of adhesion by bracts or glumes, by the pericarp of the fruit, by the calyx, and by the whole (or part) of the plant, usually bearing fruit with it, being viscid. These are mostly adhesive by resin or gummy glands. Seeds are usually adhesive by mucilage exuded from the testa, and only effective when the seed is made wet.

Viscid-glandular Bracts.—In some plants the bracts bear adhesive, viscid glands by which the fruit is attached to a passing mammal or bird. In these cases the abscission of the fruit takes place below the bracts, so that they accompany it when detached. One of these plants is *Linnaea borealis* (*Caprifoliaceae*), a small creeping plant forming a mat of foliage on the ground in pine forests in Scotland, Norway, Russia, Poland, Germany and Switzerland. The flowers are in pairs, on separate pedicels on a peduncle, about 3 inches tall. The very small fruit is 3-celled and 3-ovuled, but only a single seed is

developed, the other ovules being aborted. At the base of the fruit, and partly enclosing it, are 2 ovate bracts covered with glandular hairs, as are the pedicels (Pl. XXI, fig. 17). Thus the fruit would be readily adhesive to any mammal or bird resting on the mat, especially such small mammals as hares or marmots, and they might also adhere to the feet of a deer. Heinitz (" Om Epizoisk frospridning ") describes how he found, in Sweden, some fruits of it adhering to the fur of Hares (*Lepus timidus*), and to the feathers of Willow Grouse (*Lagopus lagopus*).

Siegesbeckia orientalis (*Compositae*) is a yellow-flowered weedy plant, probably indigenous to South America, but now largely a weed of cultivation, widely distributed over the warm and dry parts of both hemispheres. It is about 2 feet tall, very hairy, with the bracts of the involucre usually covered with viscid hairs. At the base of the involucre are 4 narrow spreading spathulate green bracts covered with glandular hairs, by which it can adhere to the hair of animals or to human clothing (Pl. XXI, figs. 2 and 3). From the distribution and frequent occurrence of this weed in cultivated ground, it is certain that it owes its widespread distribution and its abundance more to the transport by attachment to human clothing, baggage, etc., than to dissemination by animals. It has appeared, at Kew and elsewhere, in England, and has also been collected in Venice, but it was cultivated in Italy as a garden curiosity in the 17th century. It has reached the Caucasus, Armenia, Turkestan, India, Siam, the Malay Peninsula (but rarely, and only sporadically), Java, Sumatra, Philippines, Papua, Australia (in 1802), New Zealand, Kermadec Isles, New Caledonia, and all over Polynesia, Africa, Socotra, St. Helena, Madagascar' and Mascarene Islands, and South America from Mexico to Chile, and Trinidad. It is absent from all distant islands.

Leptaspis urceolata (*Gramineae*).—This is one of the very few grasses inhabiting the dense and wet forests of the Malay region. Like all such grasses, it possesses very broad leaves and adhesive fruits. The plant is from 1 to 3 feet tall, and has a terminal panicle, the branches of which spread widely, when the fruit is ripe, and are then from 4 to 6 inches long. The terminal flower in each branch is male, and below it are 3 or 4 female spikelets scattered at some distance apart. These spikelets have 2 small empty glumes at the base, and 1 which forms a pear-shaped utricle enclosing a pistil, and eventually a grain. This utricle is hard and thick, about ¼ inch long, covered with a close mass of slender hairs, very viscid when wet. Some of the hairs are hooked at the tip, but the fruit does not adhere by the hooks. I moistened one old fruit which had been collected some years, and found it adhered to my hand as if by gum, whereas unwetted ones did not do so. Except for the fruit, the whole plant is glabrous. When one brushes past this plant in the forest, the whole panicle adheres to the clothes and comes away from the plant. The wild pigs seem to be the regular dispersers of this grass, which occurs sporadically along their tracks. The plant occurs in Ceylon, all over the Malay Peninsula, Java, Sumatra, Borneo, Philippines, Amboina, Papua, and the Solomon Islands. It is absent from India and other mainlands of Asia and Africa, and from oceanic islands.

L. Cumingii, *L. cochleata*, and several other book species, all of which seem to be practically identical, have simple slender racemes with much smaller and lighter fruits, oblong rounded and thin, but covered with the same kind of glandular hairs as those of *L. urceolata*. They range from Ceylon, Celebes, Philippines, Papua, New Caledonia to Australia. This set is represented in Africa by *L. conchigera*, which closely resembles *L. Cumingii*, but has numerous panicle branches instead of a single one. It occurs in suitable places in Africa and the Comoro Islands. While fruits of *L. urceolata* are too bulky to be transported by birds, those of *L. Cumingii* and *L. conchigera*, in which the small

viscous spikelets are readily detached from the raceme or panicle, could be easily transported by them. Hence, perhaps, the wider distribution of this type, and its occurrence in islands and places where large animals are absent.

Pharus latifolius takes the place of *Leptaspis* in South America. It is also a broad-leaved jungle grass. It differs in habit in having the fertile flower enclosed in a cylindric, viscid, hairy glume, only projecting shortly from the lower empty glumes. It is certainly less well adapted for dispersal by animals than is *Leptaspis*, but is undoubtedly disseminated by some mammal or bird. It is found in Florida, the West Indies, and southwards to Brazil.

Paspalum conjugatum, Buffalo Grass, is a creeping broad-leaved grass, a native of Brazil (and perhaps also of the West Indies), which is the headquarters of this large genus. It was probably introduced early into the Old World, and is now abundant all over tropical Africa and in the Seychelles, India, including the Nicobars, Ceylon (1824), Siam, the Malay Peninsula, Java, Borneo, Celebes, the Philippine Islands and the Sandwich Islands. It reached Christmas Island between 1897 and 1904. It is, however, absent from many regions (Australia and New Zealand), and it did not occur in Fernando de Noronha.

The creeping stem throws up culms from 1 to 2 feet tall, and slender, bearing 2 very slender wide-spreading racemes about 4 inches long, with a narrow rachis on which are borne 2 rows of very small orbicular ellipsoid flat spikelets consisting of 2 outer glumes entirely covering a third enclosing the flower and grain. The 2 outer glumes have on the edge a nerve bearing a number of rather long silky hairs which are very viscous. Moistening a dry spikelet in water, it is easy to see, under a microscope, a quantity of minute globules of mucilage dissolved out in the water. It is by these mucilaginous hairs that the spikelets adhere to the feet of cattle, human clothes, and boots.

The plant is a strong rapid grower, often forming a sward, and a popular fodder plant with cattle, which, feeding on it, transport the grain, enclosed in its glumes, on their feet and legs. It is also conveyed from one place to another in their fodder. It was probably conveyed in this way to Christmas Island, where I found it in 1904 for the first time, after a bull, a cow, and some ponies had been introduced into the island. There were then only a few plants in the settlement. It is largely dispersed also by its adhering to human clothes, and perhaps also by its adhesion to the bare legs of the natives. On Mount Ophir, in Malacca, at the camping ground, on one occasion I found a single plant on the rocks by the stream at the spot where the transport coolies wash their sarongs. It must have been brought up from the lowlands, some hours' march through the forest. As the locality was unsuited for its spreading, it did not establish itself, and on visiting the spot some years later I found it had disappeared. In the narrow jungle tracks through the forests of Perak and Selangor, in the hill districts, it covers the ground for miles. No cattle could use these hillside tracks, as they are only a few inches wide, and they are not often used by men. Walking along these wet paths, one's shoes and the bases of one's trousers get covered with the adhesive spikelets. Wild animals may aid in the dissemination of this grass, but I have no clear evidence of this, and they generally avoid the narrow tracks. It is with men and cattle that this plant's dispersal is mainly associated, and it is consequently absent from islands and inland localities, which they do not frequent. It is also not to be found in dry spots, and was absent from Fernando de Noronha, Cocos-Keeling Island, and such spots, as it requires wet for the diffusion of its spikelets, which are not adhesive when dry.

Viscid Calyx. *Verbena officinalis* (*Verbenaceae*), Vervain.—The genus *Verbena* is very abundantly represented in South America, but is much more scanty in the Old World. Though several species, cultivated for their flowers, have

appeared as garden escapes in various parts of Asia, Africa, etc., no species in the genus has so wide an area of distribution as *V. officinalis*, which, though locally used in medicine, as also formerly in witchcraft, both in Europe and Africa, never appears to have been cultivated. The small flowers are borne on long erect racemes which are covered with viscid hairs, as are also the calyces. The fruit consists of 4 pyrenes, oblong and angled, the outer faces of which are rounded, while the inner faces are provided with short stiff white processes. These minute pyrenes would of themselves be adhesive, but, when ripe, the whole calyx containing them falls off from the raceme. The calyx is very adhesive to cloth and to the hairs of long-haired animals. I tried these calyces on the short fur of a cat, and they failed to adhere; but they readily adhered, as did the whole raceme, to the hair of a long-haired terrier, so that they were not easy to detach. They would also adhere readily to the wool of sheep (*V. supina* has been found in wool-washing by Thellung). The Vervain is common in England, largely by roadsides and in waste ground, and I have no doubt, from its position, that it has largely been diffused by dogs as well as by sheep and cattle.

It is found all over Europe (except the north), Morocco, Canaries and Azores, Asia Minor, through Palestine to India, Siam, China and Japan, Philippines (rare), Australia (in 1904), Rapa Island, in Polynesia, Cape Verde Islands and Africa, chiefly in mountain districts to the Cape. In North America, Bermudas, and West Indies, and the Pampas and Chile it is probably introduced. Its original home appears to have been Northern India, whence it has radiated as far as climate would allow it; but as it is found as high as 6,000 feet, on Ruenzori, it is perhaps a native of Africa. It is so much associated with cultivated ground in America and other parts of the world that it may be doubted whether it is indigenous elsewhere. It is clearly associated with the wanderings of flocks and herds. There is little doubt that it is due to the presence of the viscid hairs on the calyx and racemes also, that this species covers the largest area of any in the genus. The other species of *Verbena* which I have examined have, indeed, hairy inflorescences and calyces, but none, so far as I can see, possess any viscidity, nor do the fruits easily attach to animals, though some have apparently been to some extent dispersed by sheep, as is alluded to above.

Plumbago (*Plumbagineae*) (Pl. XXI, fig. 5).—This genus (a very widely-distributed one) is a good example of dispersal due to the glandular viscid hairs on the calyx. With the exception of a remarkable leafless broom-like bush found in Madagascar and the Aldabra Islands, Europa and Astore, the plants are all straggling herbs, with a 1-seeded fruit enclosed in a calyx covered with very sticky glandular hairs. One species, *P. europaea*, occurs in the South of Europe, Asia Minor and Palestine, another is confined to the Altai Mountains. *P. zeylanica*, probably a plant of African origin, is now spread over the whole of the Old World tropics as a weed, chiefly by roadsides and in waste ground. It is found all over Africa and Asia, in the Cape Verde Islands, Madagascar, Hainan and Formosa, and reached Australia as early as 1802. Mr. Burtt found its fruits adhering to his clothes in tropical Africa, and there can be little doubt that it owes much of its wide distribution to man, but it may have been brought to Australia in sheep's fleeces. *P. rosea* is widely distributed also, but chiefly as a garden escape, being cultivated for its beautiful flowers, and to some extent as a remedy for leprosy. The common Asiatic species is replaced in South America and the West Indies by *P. scandens*, which is common there, and occurs also in the Galapagos Islands, where it has probably been introduced by the adhesion of its fruiting calyces to birds.

Salvia glutinosa.—A large yellow or orange-flowered *Salvia*, with a calyx

over ½ inch long, very sticky, with short gland-tipped hairs, as is practically the whole plant. It is a native of Asia Minor, Syria, Persia and India. The calyces, with the enclosed nutlets, would readily attach themselves to passing animals, and thus be carried about.

Viscid Fruits.

There are a number of plants in which the fruit is provided with viscid glands or short hairs which are viscid at the tips, by which they adhere to passing animals or birds. Most of these are small plants, which can be dispersed by attachment of the fruits to mammals; a few are trees of the sea-shores, where birds (chiefly sea-birds) are the disseminating agents. In some cases (the fruits being inferior) it is the adnate calyx which is adhesive, as in the *Pisonias* and the achenes of the *Composites*. In a small number the ripe pericarp of the fruit is armed with short sticky processes.

Viscid Drupes or Berries.—Some drupes and berries have so viscid a pulp that they can readily adhere to the feathers of birds or hair of mammals, and the seeds be so borne away. Noticeably this is so in *Viscum* and other *Loranthaceae*, but these I deal with fully under the account of the Flower-Peckers (*Dicaeidae*) and other birds which disseminate these plants (*see* p. 466). Baillon in " Dissemination des graines de *Tamus communis* " suggests that this form of adhesion may come into play in this plant, the Black Bryony. He has observed that snails gnaw the berries, and, when the pericarp is bitten through, the seeds are extruded, viscid from the juice of the fruit. They may then adhere to any object, or, by falling on the ground, become fixed to it. In such a case they might stick to a passing bird or to a fallen leaf, and so be blown away with the leaf, as is described under the account of Wind Dispersal.

Among the most viscid of fruits we have those of the trees *Cordia myxa* and *C. obliqua*, of tropical Asia.

The mucilaginous coat of these is very adhesive, and native children in Singapore are fond of throwing these fruits at each other, so that they stick firmly to their clothes or skins. I have no record of their being actually attached to and borne about by birds, but should a bird fly up against them in the tree, they would certainly adhere to it. The mucilage of the fruit of the Squirting Cucumber (*Ecballium*) is also very adhesive, and would cause the seeds to become attached to a passing animal, and the seeds of *Arceuthobium*, shot out by explosion, also adhere by their mucilage; but these are dealt with under Explosive Fruits, pp. 665, 672.

One of the most interesting genera in which the fruit is very viscid is *Pisonia* (*Nyctagineae*), a genus of trees, more rarely bushes or climbers, occurring all over the warm parts of the world, but chiefly on seashores, and particularly addicted to island life. The fruits are 1-seeded, enclosed in the accrescent, and eventually very viscid tube of the perianth. They are green, and though the flowers, which are green, white, or pink, are usually contracted into a small head, when the fruit ripens, the very short pedicels lengthen, often for several inches, so that the whole infructescence forms a spreading, sticky mass. There are two forms of the fruit. In one, represented by *Pisonia aculeata*, it is short, from ½ to 1 inch long, on a long slender pedicel, oblong, with 5 longitudinal rows of close-set processes, each terminated by a sticky gland (Pl. XXI, fig. 1), in the other form it is longer, more cylindric and smooth, with no processes, but very sticky all over (*P. excelsa*).

The most widely-distributed species is *P. aculeata*, a thorny climber of no great size (with fruits as described above), which ranges over both hemispheres, occurring in Madeira, Arabia, Gold Coast, Lagos, Uganda, Kilimanjaro, Natal, Mauritius, Diego Garcia, India, Ceylon, Andamans, Siam, to the north

of the Malay Peninsula, Java, and most of the Moluccas, the Philippines, Hainan, Formosa, and the whole of America from Florida southwards to Paraguay. Allied species, with a similar structure of the fruits, occur in the Seychelles and Rodriguez.

P. excelsa (*P. umbellifera* Seem.) is a tree in which the fruits are long linear or sub-cylindric, about 3 inches long, smooth and very sticky, without the stalked glands of *P. aculeata*. There are a number of forms of this species, which seems to be variable in the shape of the leaves and in the inflorescence, and the length of the fruit, and a number also which appear to be botanically distinct, but in which the fruit is of the same type and form; but we may class them as the same for distributional purposes. They range from the Andamans and Nicobar Islands, Malay Peninsula, Java, Buru, Christmas Island, Papua, the Philippines, Formosa, Australia, New Zealand, Norfolk Island, New Caledonia, Fiji, Hawaii and most of the Polynesian Islands, and a similar type occurs also in Mauritius and the Aldabra Islands. South America and the West Indies contain a large number of species, many of which have small, oblong, smooth fruits ½ inch or more long, and one of these occurs in Fernando de Noronha (*P. Darwinii*).

These *Pisonias* usually grow near the sea, *P. aculeata* generally in sandy places, *P. excelsa* in rocky places, but occasionally they are to be met with some way inland. Thus I found *P. excelsa* growing at the foot of limestone rocks inland at Kwala Dipang, in Perak, but only 1 or 2 trees. These were in forest 40 miles from the coast. The Malays, however, affirm that in their grandfathers' time the sea came up to the limestone range, and that they tied their boats up there. It is probable that their date is wrong, but it seems certain that the lowland alluvial flat, now 30 to 40 miles across, is of no very vast age. The plant has not been found elsewhere in the Malay Peninsula, and it is clear it has not spread.

Sir W. L. Buller states that he has seen the New Zealand Fruit Pigeon (*Carpophaga novae-zelandiae*) feeding on the fruits of *P. umbellifera*, and there is no doubt that the very wide dispersal of these *Pisonias* is due to the adhesion of their fruits to the feathers of birds.

In a note on a specimen of *P. aculeata* from the Mabira forest, Chague, Uganda, Mr. C. B. Ussher, the collector, states :—" I have found a bird lying " helpless on the ground covered with the fruit of this creeper. Its feathers " were all stuck together, and it was unable to fly."

H. O. Forbes (in " The Notes of a Naturalist in the Eastern Archipelago," p. 30) says of *Pisonia inermis* (?) (probably *P. excelsa*) :—" Its seeds are spiny and " glutinous, and, by adhering in great numbers to their feathers, often prove " fatal to the herons that nest in these trees on the summit." These herons he states, are *Herodias nigripes* and *Demiegretta sacra*, both very widely-ranging birds, and *Nycticorax caledonicus*, the Australian night-heron.

R. H. Govett (in " A Bird-Killing Tree," *Proc. Inst. New Zealand*, 1883, xvi, 364) describes how in New Zealand a bush of *Pisonia Brunoniana* (which is probably a form of *P. excelsa*), about 10 or 11 feet tall and 20 feet in circumference, was found to have caught by its glutinous pods 2 *Zosterops* and an English sparrow. Later a dozen *Zosterops* were found firmly glued to the pods, and tufts of feathers showed that more had been caught. A black cat which sat beneath the bush caught a number of the birds when in their struggles they fell, but the fruits adhered to her fur, and had to be taken off her.

Hillebrand says that the Hawaiians used this gum from *Pisonia* as bird-lime for catching birds, and Guppy says he often found the fruits adhering to his clothes. He also says that the fruits do not occur in sea-drift nor floating, and they cannot be dispersed by sea-currents, as they have little buoyancy. There can be little doubt that these trees and shrubs owe their wide dispersal

to birds—chiefly, at least, to distant islands—by the reef-herons, and to such large sea-birds as boobies and frigate birds, some of which are to be found on all tropical coasts, and several species of which are of very wide distribution. Small birds would not readily get away with the larger fruits, and, getting caught, as Govett describes, would perish on the spot.

It is worth noting, perhaps, that the most widely-distributed species, often occurring some way inland, *Pisonia aculeata*, possesses small fruits which could be borne off by small birds, as well as large ones, while the 3-inch-long fruits of *P. excelsa* would depend for their distribution on the larger birds such as herons and boobies. The White-eyes (*Zosterops*), mentioned by Govett, were probably searching for insects in the tree when they were caught by the fruits. The New Zealand *Zosterops* is said to be a modern invasion, and probably, like the introduced English sparrow, was too new to the tree to avoid being caught.

Prain, in his account of the vegetation of Coco Island, Andamans, gives a curious note on *P. excelsa* :—" The path was strewn with the fruits. A tree-" snake was seen so entangled in a fallen panicle that escape was impossible, " its every movement involving it more hopelessly in the tough, sticky mass."

Boerhaavia.—This is a genus of herbaceous plants belonging to the order *Nyctagineae*, and related to *Pisonia*. The fruits are small, and covered with glandular hairs or processes, by which they can adhere to clothes, fur, or feathers. The genus, of which a large number of species (to some extent reducible) are described, occurs all over the warmer parts of the world in sandy or rocky spots, in deserts, dry rocky mountains, and sea-shores, in sand, shingle or on rocks, and on the shores of most of the islands throughout the warmer regions. Several species are abundant in cultivated grounds and around houses, evidently in these cases conveyed from one place to another on the clothes of the inhabitants. The fruits are 1-seeded, and, as in *Pisonia*, the glands are borne on that part of the perianth which encloses the ovary as a tube, and often on the persistent limb as well. They are of two forms, one in which the glands are scattered indiscriminately all over the fruit, and usually sessile, and the other in which the glands are stalked and fewer, usually a circle at the top of the fruit, and scattered ones below. In this form the fruits are more elongate, and rather larger. In most cases at least the glands only develop when the fruit is ripe, and though there are forms in which the whole plant is viscid, as a rule the glands are confined to the tips of the branches and the fruit, i.e., the adherent calyx-tube. The branches and stems of these plants spread widely, and in the American *B. paniculata* the inflorescence is widely panicled, so that the very small fruits of these species readily attach themselves to anything that comes near them. The plants are distributed all over the warm parts of the world, one, *B. plumbaginea* (abundant in Africa) being found as far north as the south of Spain. It has fruit with stalked glands at the tip and scattered ones below.

The most widely-distributed species in the Old World is *B. diffusa* (*B. repens*), which has small fruits about $\frac{1}{8}$ inch long, oblong obovate, with 5 ribs, completely covered with minute sessile glands, and very sticky. It occurs in Egypt, Morocco, Palestine to India, Ceylon, China, Liukiu Islands, Formosa, the Malay Peninsula, Java, Christmas Island, Cocos-Keeling Island, Moluccas, Philippines, Papua, New Caledonia, Australia, Cook's Island off the New Zealand coast, and all the Polynesian Islands, all Africa, Madeira, Socotra, Aldabra, Seychelles, Mauritius and Rodriguez. There is no doubt that this plant is distributed mainly by sea-birds to the islands and seashores, but in many parts of the world it is used as a pot-herb, in medicine, and cattle fodder, which is the cause, to a certain extent, of its dispersal inland. It may also persist for a long time in suitable spots formerly on the sea-coast, but now

abandoned by the sea. Thus I found it far inland in Perlis, on a limestone rock formerly an island in the sea, where still remained sea-bird guano in hollows of the rock. I have also found it on the railway track in Java, where the fruits had been undoubtedly brought in sand ballast from the seashore. *B. repanda*, also a widely-distributed plant in India, Siam, Australia, occurs in St. Helena, and *B. scandens*, common in America from Arizona to Bolivia, and *B. erecta* in the Galapagos, doubtless brought by sea-birds. Of *B. tetrandra*, Lister notes, on a ticket in Kew Herbarium, referring to Canton Island, Phoenix Group :—" The seeds of this plant were found entangled in the down " sticking to the branches of *Tournefortia* bushes, which were bare from being " the habitual preening place of Boobies (*Sula piscatrix*), which is good evidence " of its being dispersed by this far-flying and common bird " (Pl. XXI, fig. 4).

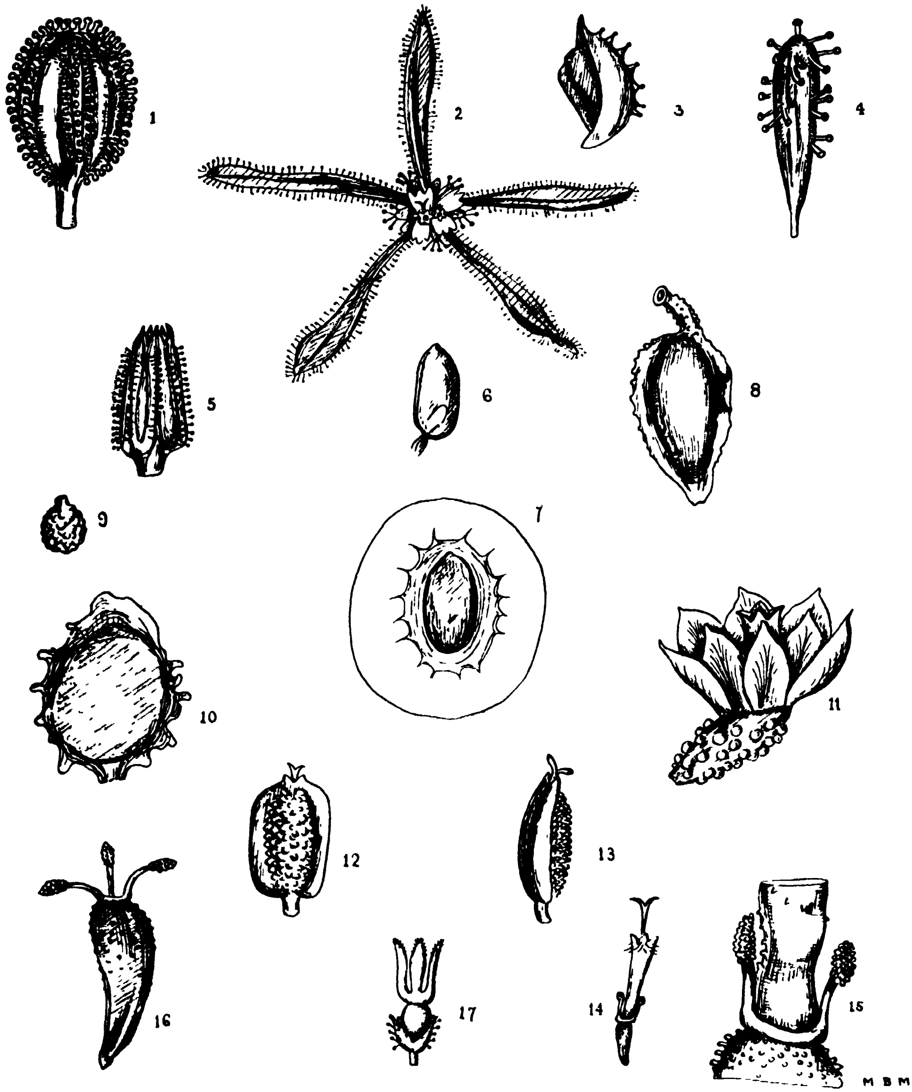
Adhesive Achenes.—In the *Compositae* the fruit, an achene, is more or less viscid from minute glands on the surface (which is, strictly speaking, the calyx-tube), or it may exude a viscid matter from the outside without visible glands. The plants are usually herbs or bushes, and animals brushing past them, or birds settling on them when the fruit is ripe, may carry off the achenes attached to their fur or feathers. Kerner states that he has seen a small owl, *Athene noctua*, which, in catching mice among the Wormwood bushes (*Artemisia* sp.), brushed against them, and when it flew away was all besmeared by the fruits which had been rendered sticky from the rain.

Pumilio (*Rutidosis*) *argyrolepis*. — This little *Composite* is well described and figured by Darwin from specimens sent from Australia by James Drummond (in the *Gardeners' Chronicle*, 1861, p. 4), with the following note :—" The achenes of several small Composite plants are blown about " by the wind till a shower of rain falls, when they attach themselves to the " soil by their lower ends by a gummy matter, at the same time settling them- " selves upright. They are not easily removed when the ground is flooded by " thunderstorms.

" The achenes possess a pappus formed of 9 scales expanded like a " flower, by which they might be easily borne to some distance by wind. " The base of the fruit is deflected at nearly a right-angle to the pappus, and " is in the form of a foot, of which the sole and toe are covered with small " bubbles, each including a minute hard ball of mucilage, which becomes " adhesive when moistened. When placed in water, the bladders burst in a " few minutes longitudinally, and discharge their contents, rendering a large " drop of viscid matter, which does not diffuse in the water surrounding the " achene. The moisture of a damp surface is sufficient to cause the bladders to " dehisce. Here the mucilage is only produced on the side of the achene that " lies on the top of the soil. If the achene lies on the side of the soil, the mucilage " is poured out on the toe, and the achene assumes an erect position." It is obvious from this that the use of the mucilage is to attach the fruit to the soil in a suitable position for germination, and this appears to be the original utility of the exudation of mucilage in all fruits and seeds ; the additional use in dispersal is a corollary to this primitive use (Pl. XXI, fig. 11).

One of the most interesting of the *Compositae*, in the matter of dispersal, is *Adenostemma viscosum*, well described by Yapp (in the *Annals of Botany*, xx, 311, pl. xxiii). The plant is a herb about 12 inches tall, with heads of white flowers on spreading branches. The fruit is an achene about $\frac{1}{8}$ inch long, more or less glandular all over, but bearing on a ring round the top 3 to 5 processes evidently corresponding to the pappus, or free parts of the calyx, which are clubbed, and the clubbed portion is composed of very viscid glands. " As in the capitula of many other Composites the torus " (receptacle), during the ripening of the fruits, assumes a more convex shape, " while the involucral bracts, which at first are erect, become spreading and

PLATE XXI.



VISCID SEEDS AND FRUITS.

FIG. 1.—*Pisonia aculeata* (fruit, enlarged).
,, 2.—*Siegesbeckia orientalis* (head, enlarged).
,, 3— ,, ,, (fruit)
,, 4.—*Boerhaavia scandens* (fruit).
,, 5.—*Plumbago zeylanica* (calyx).
,, 6.—*Luzula purpurea* (seed).
,, 7.— ,, ,, ,, (after immersion in water, after Buchenau, much enlarged).
,, 8.—*Lagenophora Gunniana* (achene)
,, 9.—*Peperomia cyclaminoides* (achene, enlarged).
,, 10.— ,, ,, (,, in section, enlarged, after Hill).
,, 11.—*Pumilio argyrolepis* (achene, enlarged, after Hooker).
,, 12.—*Cotula integrifolia* (achene, front view).
,, 13.— ,, ,, (,, side view).
,, 14.—*Adenostemma viscosum* (floret).
,, 15.— ,, ,, (portion of floret, enlarged).
,, 16.— ,, ,, (achene, enlarged, after Yapp).
,, 17.—*Linnaea borealis* (fruit with bracts, enlarged).

[*To face p.* 616.

"finally reflexed. The corollas and styles then fall off. The pappus (i.e., the "processes) now begins, usually before the actual throwing off of the "corollas, to excrete an exceedingly viscid, clear liquid, which forms a large "drop surrounding the tip of each seta (or process). In this condition the "setae bear a marked resemblance to the leaf-tentacles of *Drosera*. At the "same time the setae move from a vertical into a horizontal position." The glandular mass at the end of each seta is shown to consist of a number of capitate secreting hairs set so closely as to form a continuous gland. Yapp points out the importance to the plant of the corollas and styles all falling in a mass, as, if they did not do so, there would be a risk of some being caught by the secretion of the pappus, and impeding the action in respect to passing animals. This effect is produced by the occurrence of long filamentous hairs in the upper part of the corolla just below the lobes, which form a kind of felt which entangles all the corollas together, so that, when they fall, owing to a rupture of thin-walled cells between the thickened layers at the lower part of the corolla, and a similar thickening at the top of the calyx-ring, all the corollas fall in a mass. This plant is of very wide distribution, and is probably an original inhabitant of South America. It is found all over Africa, Madagascar, Mauritius, Comoro Islands, Bourbon, India, Ceylon, Malay Peninsula, Java, Sumatra, Borneo, Amboina, Aru and Kei Islands, Philippines, Papua, Australia, Marquesas, Fiji, Hawaii, Samoa, China, Japan, and the whole of South America and the West Indies.

In many places it seems to occur only in cultivated ground, orchards, and villages; but I have found it in the Malay Peninsula in forests as well as in villages, and even at considerable altitudes in the dense jungle, but in no place where it is impossible for it to have been carried by man. The fruits adhere very closely to cloth, and I believe that it owes its wide distribution chiefly to human wanderings. It is possible that domestic cattle have, in some cases, carried it further, but I have no evidence that it is conveyed by wild beasts. It is absent, apparently, from all oceanic islands (Pl. XXI, figs. 14, 15, 16).

Cotula is a genus of usually low-creeping *Compositae* with small yellow heads of tubular flowers. The achenes are not provided with a pappus, but are small, and either quite smooth (when, on being moistened, they exude a quantity of mucilage), or they have on one or both sides a number of glandular papillae, or, as in *C. filicula*, of Australia, the glands are confined to the remains of the calyx. In many cases the smooth achene is winged on both sides, and the mucilage is exuded from the wings. The plants inhabit damp swampy ground or dry stream beds, and are chiefly natives of the Antarctic region, Australia, New Zealand and the Cape, but are now spread all over the world (Pl. XXI, figs. 12 and 13). Their comparative abundance in the temperate oceanic islands seems to show that they owe their wide distribution to the attachment of the viscid achenes to the feet and plumage of wading or swamp birds. No fewer than 8 species, however, are recorded by Miss Hayward as appearing from wool waste in Tweedside, and there can be no doubt that they are carried about by sheep as well as by birds. As they are largely prostrate plants forming mats on the damp soil, the achenes are picked up mainly by the birds and sheep while reposing on the patches of *Cotula*.

C. coronopifolia is the most widely distributed of the species. It is a small herb about 6 inches tall, growing in wet spots, marshes, and sandy shores. The achenes are very small, flat, and light, and easily, when ripe, blown a short distance to the ground, where they may be picked up on the feet of a wading bird. They are elliptic, about 2 mm. long, flat, and on one side bear a comb-like mass of papillae in the centre. These papillae are mucilaginous when wet, and Gay, on a specimen in Kew Herbarium, says :—"Part of the wing "outside the two suture lines dissolves into a pulp with scattered filaments."

The plant is found in marshes in Europe from Norway to Spain (it has occasionally appeared in England, but only as an escape from a rockery garden), and in Morocco to Persia, the Cape, St. Helena, Australia (1802), New Zealand, and along the west coast of America from Chile to California. In most of these spots it occurs in tidal or freshwater marshes, but on the African coast of the Mediterranean it often occurs in sandy spots by the sea. The earliest record I have for Europe is Friesland (1742), and it was collected in Australia in 1802. This wide distribution and its abundance on the west coast of America suggest that its spread is not due to human agency entirely, but that the attachment of its achenes to sheep's wool may have played a part in its distribution.

C. aurea.—The achenes in warm water are very mucilaginous, says Gay, and Hooker also says they have a mucous coat. Its distribution ranges from Tunis, through the Sahara, to Egypt, Persia, India. It has been found also in Spain (Loefling), and has been met with at Bradford in England. *C. anthemoides* is rather a woolly desert plant in Egypt, India, Tonkin (in rice-fields), China, tropical Africa and St. Helena (Dillenius 1733). *C. australis* has winged achenes with glandular papillae on one or both sides, and they are recorded as being viscid. It is found in India, Australia (1802), New Zealand, Kermadec Island, Juan Fernandez, Ecuador, Vancouver Island (on ballast heaps), and Santa Catalina Isles, California. Probably it is partly distributed by sheep's wool and partly by ballast, and in many places by adhesion to birds.

The number of species is very large, especially in the Antarctic islands. The following are peculiarly insular plants which must have been introduced into the islands by sea-birds or waders: *C. plumosa*, Campbell, Kerguelen, Lord Auckland, Macquarie Islands; *C. lanata*, Lord Auckland Isles; *C. muelleri*, Chatham Isle, Stewart Isle (also New Zealand); *C. Goughensis*, Gough Isle; *C. Moseleyi*, Tristan d'Acunha; *C. villosa* and *C. coronopifolia*, St. Helena (Pl. XXI, figs. 12 and 13, *C. integrifolia*).

Eclipta alba (*Compositae*).—A small white-flowered weed of remarkably wide distribution, usually from 6 to 12 inches tall. The achenes are very small, 2 mm. long, oblong, flat, with no pappus, as the small straight sepals break off when the fruit is ripe. There are a few minute, apparently viscid, hairs at the top of the achene. The surface of the achene is microscopically papillose, and there is a sharp edge with papillae on each side. When damped, the fruits feel sticky, and under the microscope there is seen to be an exudation of mucilage. The plant occurs usually as a weed in cultivated ground, paths, etc., but is also in many places recorded as being found in marshes and on river banks. It is found in Arabia, Egypt, and Africa, as far south as the Transvaal, Socotra, Madeira, St. Helena (1808), Madagascar, Mauritius, Afghanistan, India, Siam, the Malay Peninsula, Andamans, China, Japan (on the sea-sand), Borneo, Java, the Philippines, Papua, New Caledonia, Krakatau (by 1919), Australia (1802), Fiji, Solomon Isles, Hawaii, America from Philadelphia to Montevideo, Bermudas, Galapagos, Fernando de Noronha. It is rather difficult to decide whether this plant was originally a native of Africa or of America. From its affinities, and the fact that it is largely recorded as a swamp plant in America, it appears to me to be a native of South America, and from its viscidity I think it was originally dispersed by adherence to the feet and plumage of birds, which may account for its appearance in Krakatau. But as it is very commonly found in waste ground, as in the Malay Peninsula, it owes much of its distribution also to human agency, either by adhesion to feet or clothes, or to importation with other plants.

Lagenophora.—A small genus of little *Compositae*, resembling small daisies, and growing in open spots, turf, and short grass. The very small achenes have no pappus, but are covered with small viscid glands, as is the corolla. They are natives of Australia, Tasmania, New Caledonia, Java, Sumatra, Hongkong,

India and Ceylon, and one species is native of Tristan d'Acunha (*L. commersoni*). There is little doubt that the distribution is due to birds, and, as the common plant is usually an inland one, probably to some small inland bird. In Sumatra, where I saw one species growing abundantly in the turf of the golf links, at 5,000 feet elevation, at Berastagi, the swallows were flying about just over the heads, and might readily pick up the seeds on their feet or feathers as they flew. The achenes are sticky when dry (Pl. XXI, fig. 8).

Among other *Compositae* with viscid achenes Kerner records *Matricaria Chamomilla*, and Guppy adds *Chrysanthemum leucanthemum*, and Small gives *Ch. Fontanesii* and *Ch. multicaule*. I find the achenes of the *Matricaria discoidea* are somewhat sticky when wetted, though I have seen no effusion of mucilage (*see* p. 534).

Gnaphalium luteo-album.—This pretty cud-weed is very widely distributed, and though it is certainly widely dispersed by its plumose achenes, this alone could not account for its extraordinarily wide distribution. It occurs all over Europe, as far north as Norway, and sporadically in England, the whole of Africa, Cape Verdes, Canaries, Madeira and Azores, St. Helena (1806), India, China, Formosa, Tonkin, Java, Philippines, Papua, New Caledonia, Rapa, Isle of Pines, Lord Howe's Island, Tanna, Kermadec (1854, probably introduced), Hawaii, New Zealand (1772 to 1775), Falklands, Patagonia, Chile, Bolivia (very rare), Galapagos, Mexico, and North America (not common). The large number of islands where it is found suggests that it is conveyed to some extent by birds. It is one of the eleven flowering plants found by Mr. W. R. B. Oliver on the peculiar Volcanic Island, White Island, near New Zealand, tenanted only by gannets and petrels (*Journ. Linn. Soc.*, xliii, p. 47). It is also recorded by Miss Hayward as dispersed by sheep in their wool.

The achenes of this plant are oblong or sausage-shaped, and covered with short transparent processes, which appear to be adhesive. They separate readily from the simple pappus of a few slender hairs with short upward-pointing processes, and they are hardly ½ mm. long.

Peperomia (*Piperaceae*).—These small succulent peppers are either epiphytic or rock plants. They occur all over the tropics of both hemispheres, and especially on islands. They are, however, most abundant in South America. The slender spikes of flowers produce very inconspicuous, minute, 1-seeded fruits, green or black, which project from the spike when ripe, owing to the shrinkage of the spike. The style is short, papillose or penicillate, the stigmatic hairs being sometimes clubbed. The thin pericarp of the tiny fruits is peculiar. It is covered in most species with more or less oblong papillae, between which, at the base of the space between, are glands exuding a mucilaginous substance. In some fruits the whole pericarp appears to be covered with viscid papillae. The glands above-mentioned, A. W. Hill suggests in the case of *P. peruviana*, are hydathodes, to serve for the excretion of water. He states they contain fringent contents, and says, too, that in *P. parvifolia* the cells appear to be mucilaginous. Johnson says that in *P. pellucida* the cuboid cells of the pericarp are interspersed with knob-like hydathodes or glandular hairs. In *P. galioides* I find the cells are sticky with elongated clubbed hairs, and the stigma, which is penicillate, seems composed of persistent knobbed hairs (Pl. XXI, figs. 9 and 10).

It is by these glandular bodies that the fruits of *Peperomia* are adhesive, and probably stick to the feathers of birds, and are so transported. The plants are usually local and distantly diffused, and by no means abundant in quantity. They often grow on tree trunks, and in clumps on rocks, more rarely on the forest ground, and in damp and shady spots. Though found on many islands, they do not occur near the sea, but in the inland woods, and are, so far as I have seen, quite absent from dry coral atolls. *P. pellucida* (*P. exigua*) is a small

terrestrial species introduced from South America, and now run wild from botanic gardens in many parts of the world, but it seems to be wild also in Africa. In the East Indies it is chiefly carried about in pot plants.

Some of the other species are widely spread—*P. reflexa*, India, China, Java, Norfolk Island, Howe's Island, Australia, New Zealand, Hawaii and Africa, and Socotra; *P. Heyneana*, Bonin Island, China, India; *P. dindigulensis*, Formosa, China, Malay Peninsula, India; *P. endlicheri*, Auckland, New Zealand, Kermadec Isles, Norfolk Island; several species in Hawaii, and there are some in most Polynesian islands. Two species are found in Christmas Island (besides *P. exigua*, accidentally introduced from Singapore), one endemic and one Javanese, both epiphytic. I cannot see how these plants reach oceanic islands except by adhesion to birds' feathers.

Piper umbellatum (*Heckeria*), a tall large-leaved pepper with cylindrical spikes and small fruits something like those of *Peperomia*, a shady rock plant in forests in India, Malay Peninsula and islands, Australia, South America and Africa, probably has the small fruits viscid also. It appeared in Krakatau in 1919, and must have been brought by birds. Guppy says that *Piper Macgillivrayi* of Polynesia also has adhesive fruits.

Some of the small-seeded urticaceous plants owe their distribution to oceanic islands by the achenes being attached by their viscidity, when damped, to birds. In Christmas Island we have one of the small herbaceous nettles, *Fleurya ruderalis*, which is found also in some of the Moluccas, Java, and other islands. It was found there by Lister, in the voyage of the "Egeria," before any people had settled on the island, consequently it could not have been brought there by man. I noticed, however, that it was only to be found there where the fishermen used to go to fish, and it is at the present day certainly distributed by them, the viscid achenes adhering to their clothes. The common Malayan species is *F. interrupta*, which has slightly larger achenes, distinctly viscid. It occurs sporadically about villages and cultivated grounds.

Another plant in Christmas Island with viscid achenes, belonging also to the *Urticaceae*, was *Boehmeria urticans* (*B. platyphylla* of the Expedition to Christmas Island, from which, however, it is distinct). This is a shrub or treelet, 18 feet tall. The achene is enclosed in the utricular perianth, which is viscid-hairy. Unlike other species of the genus, the plant stings as badly as the Tree nettle (*Laportea*).

Labiatae.—A considerable number of the herbs of the order *Labiatae* have viscid nutlets. They do not appear to have any glands on the nutlets, but exude a quantity (often very abundant) of mucilage when wetted. Kerner mentions (as possessing this property) those of the Basils (*Ocimum basilicum*) and other species, *Salvia* and *Dracocephalum*; Guppy adds *Prunella vulgaris* (as does Dymes), *Nepeta glechoma*, *Salvia verbenaca*, *Thymus* and some *Lamiums*. He also states that *Lycopaeus europaeus* has nutlets viscid when dry. This plant, however, is more regularly dispersed by water. The genus *Hyptis*, of which two species are widely distributed in the tropics, has also mucilaginous nutlets, and probably many more of the same order.

The Basils (*Ocimum*) are widely distributed as cultivated plants, from their spicy flavour, and have been known in cultivation for very many years. I have never seen any wild specimens. The nutlets are rounded at the tips, the testa slightly papillose. As soon as they are touched with water, they exude mucilage, and in a few minutes are covered with a thick coating with radiating points. The widely-distributed *Hyptis suaveolens* and *H. brevipes* may owe their dispersal to their mucilaginous nucules, but I have dealt with these in the Attachment to Birds and Mammals by the Calyx (*see* p. 575).

Cadaba juncea (*Capparideae*).—The Capers usually have round or sausage-shaped berries, and in *Cadaba* the fruits are long cylindrical ones, which

usually dehisce, and emit rather long-shaped seeds. They are abundant in Africa, and are also found in Australia and Eastern Malaya. The species which live in these regions are not viscid, but *C. juncea*, a native of South Africa, which is a stout shrub with long terete leaves, and which grows on rocks and precipices, has the long cylindric fruit covered with viscid stalked glands. *C. longifolia*, with lanceolate willow-like leaves, a native of Arabia, Aden, and Socotra, has small, rounder fruits ½ inch long, and appears also to possess the same kind of glands.

Aneilema protensum (*Commelinaceae*).—This genus of weedy herbs is widely spread over the world, occurring in open country for the most part, few being met with in forest. Two of the species have the fruit capsule, which is very small and rounded, covered with viscid hairs, *A. protensum* and *A. vitiense*. The former has long, slender, few-branched panicles with scattered fruits thickly covered with the sticky hairs, some straight and some hooked, as in *Desmodium ormocarpioides*. The branches, too, of the panicle are so provided, and the whole attaches itself to man's clothing, as he walks along the forest paths, and breaks off from the plant. It is found in thick forests, usually by path-edges, in the Himalayas, Ceylon, China, the Malay Peninsula, Sumatra and Java. The whole plant is from 1 foot to nearly 2 feet tall, and it is dispersed throughout the woods by wandering animals or ground birds, such as the Argus pheasant or the jungle rails. The other species with similar fruits is a native of Fiji.

Viscid Seeds.

There are a number of plants with pulpy fruit that dehisce and emit a mucilaginous mass containing the seeds, which may adhere to mammals and birds. The aquatic plants known as *Ottelia* (*Hydrocharidaceae*), on disintegrating, discharge the mass of seeds in a mucilaginous lump, which may be readily attached to water-birds, and so conveyed from one pool to another. The Asiatic *O. alismoides* is a rice-field and pool plant, and it is difficult to see how it would otherwise get from one pool to another. It is widely distributed over India, the Malay region to Japan, and Africa. Schweinfurth (in the " Heart of Africa," p. 121) says of the yellow-flowered *Ottelia* (perhaps *Boottia scabra*) that the seeds grow, like those of *Nymphaea*, in a gelatinous mass.

Guppy (" Thames as an Agent for Plant Dispersal," *Journ. Linn. Soc.*, xxix, p. 344) says of *Hydrocharis morsus-ranae*, the Frog-bit, that the seeds sink in water, and " one would hardly regard them as able to stand a bird's digestion. " When the fruit bursts, the gelatinous pulp containing the seeds is discharged, " some of which sinks slowly, while some of it adheres to a portion of the " fruit. This material would be very likely to adhere to the plumage of a bird " sitting in the water, and, in drying, the seeds would be firmly attached." This is quite possible, but direct evidence that it is so carried is desirable. The frog-bit, like the *Ottelia*, is a ditch or pool plant, and it is difficult to see how it can get about otherwise. In all these plants which grow at the bottom of the water it is essential that the seeds should sink, for if they floated they would be drifted up on the mud, where they could not develop, and if they are not swallowed and evacuated unharmed by water-fowl, there seems no other method of dispersal, except by adherence.

In *Villarsia* (*Limnanthemum*) *nymphaeoides* the seeds are fringed with hairs, and Guppy has shown that they will adhere to a duck's plumage and so be carried about; but, as he points out, the seeds of other species of *Limnanthemum* are not so furnished.

Kerner points out that many seeds possess a mucilage which only appears when the seed is moistened, and that the primary use of this is to cement the seed to the soil, where it will germinate.

Griffiths (in "A Novel Seed Planter," *Torrey Bot. Club*, 1902, p. 164) gives a good account of the use of mucilage in this way in the case of *Plantago fastigiata* in Arizona. The plant seeds heavily in March, and yielded 1 ton to the acre. In April seed was ripe, and in May scattered all over the plains. The seeds were covered with the mucilage, which is more pronounced in this and other dry-land species than in the ones which grow in damper spots, and the whole seed, when wet, is closed in a jelly. Masses of seeds collected on depressions, at first a mass of seeds in mucilage and debris. After a time the seed separated, largely from the refuse, and a crust was formed above and below, the upper layer formed by evaporation, the lower by mixing the dryer earth with the mucilage, the earth absorbing the water. Thus cakes of seed and debris were formed, often 2 feet wide and 3 inches thick. These seeds probably perished, but of seeds which were not washed together, every one was sunk in a little pit, the walls and bottom of which were rigid by the hardened mucilage. The seed was not covered then, but would be covered later by silt and sand. The primary function of the mucilage is to bury the seed, which is effected by the contraction of the expanded mucilage (which is firmly attached to its inner and outer edges) to the particles of soil, resulting in a compacting of the grains of soil to form a pit, but it is clear that it would also attach it to the feet of an animal.

Many small seeds are primarily dispersed by rain-wash or by wind, and seem to have developed the viscidity of the testa to cause their arrest, when washed or blown over the ground. In dry localities, or in dry seasons, the seeds may be blown along sand or dry soil till they reach a spot sufficiently damp for them to exude mucilage and to grow. In fact, this viscidity in seeds replaces the processes or spines utilised as anchors in wind-dispersed fruits.

Kerner points out that only smooth-coated seeds have this mucilaginous testa; those with a pitted or rough, scrobiculate surface, which can fix themselves to the soil by the roughness of the seed-coat, are not mucilaginous. Though this is the primary use of the mucilaginous testa, it is also very frequently utilised in other ways. Seeds thus provided may become attached to dead or fallen leaves, which may be blown by the wind to great distances. I have mentioned this system under the section of Wind-Dispersal, and given instances of the dispersal of *Oxalis acetosella* and *Adoxa* seeds being so disseminated (*see* pp. 22 and 23). Dymes (in "Nature Study of Plants," 1920) says that the seeds of *Prunella vulgaris* and the Brooklime (*Veronica Beccabunga*) are so dispersed, giving a figure of 3 seeds of the latter plant attached to a willow leaf. He also mentions finding 2 seeds of *Geranium Robertianum* adhering to two different leaves.

Mucilaginous seeds are also largely adherent to birds and animals' feet, feathers or fur, as are viscid fruits. Indeed, some genera, *Juncus* and *Luzula*, seem to owe their wide distribution mainly to this property. I may note here that many seeds retain their viscidity, if kept dry, for many years, only discharging the mucilage when wetted.

The following seeds are known to possess viscidity:—*Linum* (some species), *Lepidium sativum* and *L. apetala*, *Camelina sativa*, *Teesdalia*, *Arabis Thaliana*, less often *A. albida* (Guppy); *Capsella Bursa-pastoris*, *Senebiera*, *Helianthemum vulgare*, *Viola tricolor* (Guppy says that other species of the genus possess no viscidity), *Oenothera albiflora* (Clarke and Fletcher in "Farm Weeds of Canada"), *Plantago lanceolata*, *P. major*, *P. maritima*, *P. fastigiata*, and probably all species in the genus, *Erodium cicutarium*, *Geranium Robertianum*, *Veronica beccabunga*, *Gilia* and *Collomia* these emit the mucilage very speedily, on being wetted, in the form of fine threads, and *Gilia squarrosa*, and probably other species are widely dispersed in South America by attachment to sheep's wool), a number of small *Urticaceae*, *Fleurya*, etc., *Peperomia* and some species of

Piper, *Luzula campestris*, and *Juncus tenuis* ; the other species of *Juncus*, *J. bufonius*, *J. communis*, *J. glaucus*, *J. squarrosus*, according to Guppy, are much less viscous. In most of these rushes I have not been able to detect any effusion of mucilage at all, but seeds vary very much in many cases as to the rapidity of discharge, amount and conspicuousness of their viscosity.

An interesting case of seeds transported by adhesion due to viscid exudation is that of *Clitoria cajanifolia* (*Leguminosae*). This is a bush about 4 feet in height, with large and showy pale violet flowers. The pods dehisce along the upper edge and expose a number of small round peas, which are covered with a viscous resinous exudation. The plant is a native of Brazil, and in the early part of the 19th century was apparently introduced into Java as an ornamental shrub. The seeds, which are not thrown out of the pod by dehiscence, are readily attached to the hair of passing animals, and the plant was almost certainly introduced in this way into Malacca before 1844, and also into Singapore, where it is very common along roadsides and in open places where cattle pasture. From Singapore it was conveyed to Johor, and a planter there, Mr. Larkin, told me it did not reach his estate on the Tebrau River till cattle had been imported there from Singapore. It travelled in the same way to Borneo from Singapore, and is now abundant at Kuching, in Sarawak, on roadsides where cattle wander. From these spots it has not migrated to any distance, and has not travelled up the roads through the Peninsula, where ox-transport is very common, though it has reached Selangor and Negri Sembilan. It is evidently transported by cattle only, and does not travel fast.

Two other species of the genus of *Clitoria* have similar seeds, one of which, *C. glycinoides*, is a herbaceous climber, widely spread over South America from Mexico to Peru and the West Indies ; and the other is a bush, *C. stipularis*, of more limited distribution. The former probably owes its wide distribution to domestic cattle. As the seeds are held on the bush from 2 to 4 feet above the ground, it would be necessary for a large animal to play the part of disperser, and the only wild animal likely to act in this way nowadays would be a deer ; but at a much earlier date there was a larger fauna of big mammals in South America than there is now.

It is noticeable that in these plants where the seeds are raised well above the ground on the bush, they are gummy of themselves, and do not exude mucilage only when wetted, as do those of low herbs. If the seeds did not become adhesive till they reached the wet ground, their adhesive powers would be ineffective.

Plantago (*Plantagineae*).—This genus is practically cosmopolitan. Very abundant in temperate climates and dry areas of the hotter climates, it is only absent from the tropical rain-forest region and the extreme Arctic region. A very large number of species are recorded, but many of these may be reduced to a modified form of widely-diffused species. They are herbs (more rarely low shrubs), in which the small wind-fertilised flowers are borne in longer or shorter spikes, with small many-seeded capsules. The seeds are viscid when wetted, and can adhere to the fur of animals and plumage of birds. Being small and light, and borne on long slender peduncles, very flaccid, they are easily dispersed to a considerable distance by wind, and some species certainly owe their wide distribution largely to human agency, the seeds being used in medicine and for food of caged birds, and are readily dispersed by being carried on cultivated plants.

The most widely-distributed species is *Plantago major*, which ranges over Europe, temperate Asia, China, Japan, India, the Malay Peninsula (1830), Java, Sumatra, Tonga, Easter Island, Samoa (1850), Africa, Bourbon, Madagascar, Mauritius Rodriguez, St. Helena (1810), North America, Bermudas, South America, Galapagos (1905), and Juan Fernandez (1876). I include under this name a number of plants which have been separated as species, such

as *P. asiatica*, *P. robusta*, *P. tanalensis* (Madagascar), *P. cucullata* (Juan Fernandez), all of which seem to me to be local forms. In many places it has been introduced by human agency. In Fernando de Noronha it was found about gardens, and in the Malay Peninsula round Chinese huts. In Sumatra I found it in potato grounds. In both hemispheres it has a reputation as a medicine for coughs, wherefore the Chinese carry it about, and undoubtedly brought it to the Malay Peninsula. It is also used largely in bird seed, and birds being often carried about in cages, the sweepings of the bird cage being thrown about may thus introduce it. The seeds may also be conveyed in pot plants, or in mud attached to potatoes or other roots. They are very viscid when wet, and readily adhere to birds, either to their plumage or in mud on their feet, or they may be similarly carried by domestic cattle and sheep. Guppy (in "Naturalist in the Pacific," p. 276) says:—"When experimenting on these plants in 1892, I found that "the wetted seeds (of *Plantago*) adhered firmly to a feather, so that it could be "blown about without being detached, and my readers can readily ascertain, "by a simple experiment, that a bird pecking the fruit-spikes in wet weather "would often carry away some of the sticky seeds in its plumage. Several "years ago, when I was endeavouring to examine the condition of these seeds "in the droppings of a canary, my efforts were defeated by the bird itself, "since, in spite of all my care, some seeds and capsules were always carried "by the bird on its feathers into the clean cage reserved for the experiment." *P. lanceolata*.—The same methods of dispersal as mentioned in the case of *P. major* apply to this plant, except that the seeds are not used as caged-bird food, and, so far as I know, it owes nothing to human agency as a medicine. It is not so widely dispersed as *P. major*, though it is common in Europe and temperate Asia. It is also found in the Canary Islands, Madeira, Azores, Bermuda, Hawaii, New Caledonia, New Zealand, Mauritius, and the form *Azorica* in Australia (1854). No doubt in many of these localities it owes its introduction to accidental human agency. *P. coronopus*.—Common on sea-shores and inland sandy spots in Europe, occurs in Madeira and Canaries, and was (in Australia, perhaps) brought in ballast in 1844.

A very singular plant is the Cataract Weed of the rapids of Lake Tana in the Sudan, and Abyssinia, *Rotala repens* (*Lythraceae*).—This plant is described by G. W. Grabham and R. P. Black in the Egyptian Government Report of their mission to Lake Tana (1925). It is a floating plant, growing in large masses, attached to rocks in the rapids. Its fruit is a small capsule with minute seeds. When the stems of the plant are exposed above the water, the little capsules burst. If a seed is put into water, after a short time hairs are seen to grow from the original smooth testa. These hairs may attain a length equal to half the diameter of the seed. They have clavate tips, covered, as it seems, with a mucilage which would glue them down to any wet body where they might alight.

Of *Lawia zeylanica* (*Podostemaceae*), growing on rocks in streams in Ceylon, Willis records that wading birds often walk over the thalli of this plant. The seeds, when wet, are mucilaginous, and may readily adhere to the feet of the birds. These plants only flower and fruit when the rocks are bare of water.

As many of our *Luzulas* and *Junci* were found very early in the Antarctic regions, and all the other genera of the order appear to be Antarctic, I conclude that the whole order originated in the Southern hemisphere, and that gradually some of the genera migrated north, where in the temperate regions they developed into a large and abundant number of species. Specimens of what appear to be Rushes (*Junci*) have been found in Miocene beds in Europe; but as these plants appear to preserve badly as fossils, the specimens were few (and these doubtful) in Europe in Pleistocene times. The only ones found by Mr. and Mrs. Reid seem to be Neolithic in age.

The abundance of plants of these genera in all cool parts of the world seems to show their ready distribution. It is possible that in some cases the rushes may have been aided in their migrations by man, by the seeds being conveyed in fodder or packing, or, in the case of *J. acutus* and *J. maritimus*, in ballast; but I do not think that this has been of great importance in their migration, nor would it account for the very wide distribution of such plants as *Juncus bufonius* or *Luzula campestris*. The only method of wide distribution that we have is in the attachment of the seeds to birds' feet or feathers by the mucilage, and in mud. For limited distribution we have Dispersal by Wind and Rain-wash, and by Floating Seedlings. It is quite conceivable that these seeds might be conveyed long distances by the attachment to the feet of far-wandering birds, such as waders and ducks, and most of the widely-scattered species inhabit muddy wet spots where such birds go. We can trace the line of some of the species, e.g., *J. bufonius*, and *J. effusus*, northwards, via the Philippines, to Japan, and so to the Northern Hemisphere, or via South America, and so to the northern temperate regions, and from the Miocene fossils we may conclude this migration to some extent took place in early Miocene, or perhaps Eocene, days.

Luzula.—These are herbs with loose or condensed panicles of small flowers and capsules, containing numerous seeds, little over 1 mm. in length, and with a tendency to become viscid and sticky when wetted (Buchenau "Pflanzenreich," 1906, pp. 25–30). There are a large number of species and forms scattered widely all over the cooler parts of the world, chiefly in America, Europe, and North Asia. They inhabit woods and open grass pastures, but not swampy spots, as do *Junci*. Many species have a kind of caruncle on the seed formed by the funicle, e.g., *Luzula multiflora*, and this is attractive to ants, which transport the seeds to short distances. I have elsewhere recorded finding panicles with seed used as nesting material by sparrows, (*see* p. 512) but these methods of dispersal cannot altogether account for the very wide distribution of these plants, nor for their occurrence on islands. *L. campestris* is the most widely-distributed species in the world, occurring in Europe and temperate Asia to the Kurile Islands, India, Madeira, Azores, mountains of tropical Africa, Australia (1802), New Zealand (1768), Hawaii, Fiji, North and South America to Chile, the Auckland, Campbell and Macquarie Islands. In the Canary Islands are 3 species, 2 also found in the Mediterranean region, and one of these endemic—*L. purpurea*—is known to possess mucilaginous seeds. The Azores contain, besides *L. campestris*, *L. elegans* (*L. purpureo-splendens*), an endemic species; in Madeira *L. Seubertii*, endemic, and in Masafuera *L. racemosa*, also a native of the Andes of Bolivia. It is clear that these insular occurrences can only be due to bird transport, and that the mucilage plays an important part in causing the seeds to adhere to the plumage of birds (Pl. XXI, figs. 6 and 7).

Juncus.—The Rushes are even more widely distributed than *Luzula*. Their seeds are small, smaller than those of *Luzula*, and viscid when wet, and, except in one or two cases, possess no caruncle. Guppy gives them as only 0·33 mm. long. Seeds of rushes have been found by Darwin and others in mud adhering to the feet of birds, and the former records the discovery of seeds of *J. bufonius* adhering to the leg of a woodcock; and Kerner also mentions finding those of *J. bufonius*, *J. compressus*, *J. lamprocarpus*, on the feet of birds. The plants almost invariably grow in marshy spots, edges of streams and seashores, where they are likely to come into contact with the feet or plumage of birds. Guppy writes :—"It is highly probable that a bird, brushing against such plants in "wet weather, would carry off on its feathers a number of the wet seeds "of *Luzula* and *Juncus*, and that they would adhere firmly to its feathers when "dry. At least 9 species in the Azores display this property in their seeds,

" and several species most widely distributed over the world are known to " exhibit it."

Buchenau mentions as species possessing viscid seeds:—*J. filiformis*, *J. glaucus*, *J. acutiflorus*, *J. lamprocarpus* and *J. brachyspathus*, all of which, except the last, are of extraordinarily wide diffusion.

I have referred to the adhesion to birds' feet in mud, when dealing with that subject and under the account of Isolated Ponds. The distribution of *Juncus* reminds us at once of that of *Scirpus*, but with this difference—that the species in the tropics, though similar to those of the temperate regions, are largely disseminated over the high mountain chains up to 6,000 feet or higher, which is unlike the distribution of *Scirpus*. I have found *J. lamprocarpus* on volcanoes in Sumatra at over 5,500 feet altitude, and other species occur in similar isolated positions.

Juncus effusus, including *J. conglomeratus*, the most common Rush in the British Isles, is also common in Europe, Morocco, Asia Minor, Persia, India, Ceylon, China, Japan, Sumatra, Java, Philippines, Ruenzori (Africa), Madagascar, Australia (1802), New Zealand (1833), and in the islands of Canaries, Madeira, St. Helena (formerly, but now disappeared), Amsterdam and St. Paul.

The Sumatran and Javanese mountain plants are not at all typical, and are stated by Buchenau to be a hybrid between *J. effusus* and *J. glaucus*; but the latter species does not occur in the Malay region at all. It is quite possible that in a few localities the plant may have been introduced in fodder, but certainly not so in most of these places.

J. bufonius is a dwarf species with viscid seeds, common in muddy spots, and especially in shallow muddy runnels by roadsides, and is abundant in Europe, Morocco, Egypt, Asia Minor, India, Cape (1811), Australia (1802), New Zealand (1824), North America, Jamaica, Mexico to Patagonia, and in the islands of Azores, Madeira, Canaries, St. Helena. This is possibly introduced into South America and Australia on the feet of sheep or cattle, but there is no doubt it is mainly disseminated by birds.

J. lamprocarpus.—A short tufted plant with viscid seeds. Distribution: Europe, North Africa, Madeira, Azores, South Africa, Sumatra (high up on volcanoes), Philippines, New Guinea, China, India, Australia (1900), New Zealand, North America in New England and Michigan (probably an introduction, as I take it to be in Australia and New Zealand).

J. maritimus is a seashore and sand-hill species found in Europe, Morocco to Egypt, Socotra, Asia Minor, Scinde to Afghanistan, Azores, Africa to the Cape, Australia (1802), New Zealand (1824), North America (in one spot only), Bermudas, Brazil. It is recorded for the Canary Islands by Kunth, but no later botanist has seen it there. *J. acutus* is a plant of similar habitat occurring in Europe, Algeria, Asia Minor, Madeira, Azores, Canaries, Cape Verde, Africa to the South, North Asia, California, South America, Bermudas and Juan Fernandez. Both these seashore plants may be sea-dispersed by fragments of the rhizome, or in ballast, or attachment to the feet of birds. There is no doubt that the Junci have derived their wide distribution partly from the exudation of mucilage from the seeds, and then by adhesion to wandering birds. The local abundance of the riverside species is due to the dispersal of floating seedlings.

Other island species are *J. tristanianus*, Tristan d'Acunha, endemic; *J. scheuzerioides*, Kerguelen; *J. microcephalus*, *J. chamissonis*, and *J. Dombeyanus* in Juan Fernandez; *J. marginatus*, Bermudas; *J. capitatus*, *J. glaucus*, *J. supinus*, Azores.

Juncus tenuis, which has viscid seeds, was collected by Don in Clova, Forfarshire, in 1795-6. It then seems to have disappeared from Britain till Towndrow found it in England in 1883, since when it has been recorded as

abundant in 31 counties. In most localities it is said to grow by paths or roadsides, and Druce states that it is usually introduced in American forage. However this may be in the first instance, it is clear that it has been found in many localities where American forage could never have been carried. It has also been found sporadically in Holland, Belgium (1824), France, Germany, Madeira, Cape Verde Islands, Azores, Tristan d'Acunha (Macgillivray, 1852), Assam (Griffith), Australia, New Zealand (1877), and North and South America and Bermudas.

As it is one of the species with viscid seeds, it is probable that it owes its distribution largely (especially in the islands) to adhesion to the feet of birds, and along the tracks in England and Scotland to adhesion to the feet of man and cattle. In America, its original home, it is chiefly a marsh and river-bank plant.

Under viscid seeds it is perhaps advisable to speak of those of *Scaphium*, a big tree of the order *Sterculiaceae* (of which a few species are found in Burma and the Malay Peninsula), although its highly mucilaginous testa may play no part in dispersal. The seeds, which are ½ to 1 inch long, and oblong in shape, are borne singly at the base of a boat-like herbaceous carpel. These are drifted to a distance from the tree by wind (*see* p. 72). The seed, which has a thin testa, when in contact with water exudes a very large quantity of mucilage, sufficient to fill a small cup, consequently it is known to the Malays as "Kembang Semangkok," or "Fill-Cup," and, as it contains bassorin, it is used as a drug. Schomburgk mentions that in one spot in the Siamese forests the amount of mucilage exuded by the fallen seeds was so extensive that his horse was quite unable to pass over the slippery ground. The use of this mucilage may possibly be to fix the seed to the ground; but I think it would be of more advantage for the seed to roll farther away from the tree, or it might serve to protect it from the attacks of termites and other insects, or attach the seed to the feet of a passing wild beast, but I have no evidence to support either way.

CHAPTER IX

DISPERSAL BY HUMAN AGENCY

Methods by which Alien Plants are commonly introduced by Man—Dispersal of Weeds in Cereals and Vegetable Seed—in Dust Carts, etc.—London Building Sites—Ballast, Soil Export, Transport of Road Material, Fodder—Plants introduced in Packing Material—Drug and Dye Plants—Some interesting Cases of Dispersal by Human Agency—Conclusion.

THE dissemination of plants by man, directly or indirectly, is of considerable importance, not only from the extensive way in which plants have been carried from their original homes to all parts of the world, especially within the last two or three centuries, but also because this agency frequently accounts for the appearance in many countries of plants which seem to be indigenous, but yet are of comparatively recent introduction.

I reserve the word *indigenous* for plants which arrived at their present stations by natural methods, by wind, or wild animal transport, or were evolved from ancestors which were brought there by such agencies.

Formerly a large number of plants were recorded in botanical works as *Cosmopolitan*, a word accepted as meaning that they were to be found in any part of the world where the climate and environment were suitable to their growth. I have paid special attention to this class of plants (i.e., those of especially wide distribution), and find that, in flowering plants, the greater number owe their primary distribution to accidental or intentional human transport, though, when they arrived at their new home, they were usually still further dispersed by natural causes. This, however, does not apply to *Cryptogams*, which are dispersed by man to a much smaller extent than flowering plants, and which owe their wide distribution mainly to their light spores being diffused by wind.

In the study of the distribution of flowering plants, or the investigation of the flora of any region, the possibility of the action of man must always be taken into account. Deductions from statistics that include plants which have been moved or introduced by man are necessarily misleading and erroneous in establishing the geographical and historical accounts of a flora or a species. The spread of plants introduced by man into a new country varies greatly. A large number, such as garden roses and sunflowers, still remain confined to cultivated ground where man has placed them; others, such as the American *Lantana mixta* and *Ageratum conyzoides*, now spread widely over the whole world (perhaps only once introduced by man), have by this time so thoroughly established themselves by natural agency, as opposed to human aid, that they now form a part of the flora of the Old World, distinguishable from the indigenous flora only by their known history. Plants have accompanied man in this method in all directions, from North to South, or from East to West, or *vice versa*. Of the vast number which have been carried

about by man, of late years especially, comparatively few have as yet established themselves. By the *Establishment* of a plant is meant its continuous reproduction by natural agencies. Seeds and spores of many plants are transported to other localities by natural as well as human agencies, but for several reasons fail to continue their reproduction. They may fail to germinate, or, if they do arrive at maturity, may fail to produce fertile seed, or they may be exterminated by competition with other plants, or by unsuitability of climate or environment. In other words, they fail to *establish* themselves as an element of the flora of their new country.

It is quite common to find single plants (or even numerous specimens of an introduced plant) apparently flowering and fruiting well for a year or more, and then suddenly entirely disappearing having failed for some reason to establish themselves. Thus in 1890 I found plants of *Spilanthes acmella* and *Hibiscus abelmoschus*, introduced plants, in Christmas Island. By 1897 they had quite vanished, and have never been seen there since; but *Digitaria sanguinale* and *Eleusine indica*, which were there at the same time, evidently also human introductions, still persist in abundance. On Mount Ophir, at the spring where drinking water is obtained, and the transport coolies wash their clothes, I once found the common, widely-dispersed American, *Paspalum conjugatum*, the adhesive fruit of which had evidently been carried there on the men's clothes. It was flowering and fruiting, but, owing to some unsuitability in the environment, failed to establish itself, and there was no trace of it when I visited the spot some years later.

It may happen that an introduced plant may remain confined to one spot for many years, and that by some change in its environment, or from some rather obscure cause, it may suddenly start and quickly spread over a large area, becoming from a rare and local species a common and active-growing one. In most cases this seems to be due to a change in environment, but it is quite possible that, after a lapse of years, a form may arise which is able to combat the causes which restrict the spread of the species.

In Singapore there was, for many years, a patch of the American grass *Axonopus compressus* growing along the roadside near the Botanic Gardens. This was the only known patch of this grass in the Malay Peninsula. It occurred to me to utilise it as a broad-leaved grass for flower-border edges, and I had some of it dug up, and propagated and planted in the Botanic Gardens. In a few years it had spread, not only all over the Gardens and along the roadsides all over Singapore, but into the Malay Peninsula as far as Selangor. The original patch had been hemmed in by stronger-growing creeping grasses, so that it had been quite unable to spread; but as soon as it reached a spot where there was little or no competition, it was able to spread, and actually drove out the other grasses. Another case is that of the Composite *Senecio squalidus*, a native of the volcanic rocks of Sicily and South Italy, and by no means a common plant, even in its own home. The plant was introduced into the Oxford Botanic Gardens in 1699. A century later it grew on more of the Oxford walls (1799), and by 1833 had reached Wytham. When I was an undergraduate at Oxford in 1875, we only knew of it growing on walls in the corner of the town known as Jericho. It eventually reached the railway track (1877). "The track was made of clinker ash, which suited the plant "as much as the lava soil in its home on the Sicilian volcanoes." Druce, from whose "Flora of Oxfordshire" I take most of its story, writes:—"I have seen "them (the plumed achenes) enter a railway carriage near Oxford and remain "suspended in the air till they found an exit at Tilehurst." It then, travelling by train, reached Reading, where it is now extremely abundant on the walls of the ruined Abbey and elsewhere. It got to Swindon in 1890, and went on to Bristol, Cardiff, Fishguard and Cardigan. It is recorded as plentiful in Bletchley

in 1915, and reached Denbighshire in 1916. In 1922 I found fine plants of it in an old football field, which had just been ploughed up, at Mortlake, in some abundance; but since (as Druce remarks) it dislikes any other plants near it, it has since been nearly exterminated by the occurrence of ordinary weeds. This was its first appearance in Surrey, and it was certainly not to be seen in that locality between 1912 and 1922. On the Continent it does not appear to have spread at all, but has occurred, probably as a garden escape, in Devon, Cork, Spain, Portugal, and Transylvania. This formerly very scarce and local species is now more common in England than anywhere else in the world, and this seems mainly due to the use of clinkers on the railway banks, and the seeds having been blown on to the passing trains.

A large number of works and papers have been published on the alien plants of different parts of the world, and it would be impossible to give a full account of the innumerable species which have found their way from one corner of the globe to another by the aid of man, and to have established themselves. Even in the lowlands of the tropics, where man has settled, it is now quite common to find a very large portion of the ground occupied by alien plants from the other side of the globe. In Ceylon I have had to walk many miles before I could get out of the area of South American weeds. In Dunn's "Alien Flora of Great Britain" (1915), a very large number of plants introduced by man into Britain are recorded. A large number of them, however, have only appeared once, and then vanished, having failed to establish themselves. Every year additional species are recorded as intentionally brought into the country, having escaped from cultivation or been accidentally introduced. They come from all temperate regions of the world, and sometimes settle and form part of the flora, though it is surprising how many plants may grow readily and reproduce themselves in a garden till they amount to a pest, and yet utterly fail to establish themselves outside. *Oenothera biennis*, the evening primrose, grows and reproduces itself readily in the garden without any attention; but it has not become abundant generally as a wild plant, except on the sand-hills of Lancashire and a few other spots, and has been mentioned in Victoria, Australia, as making slower progress than the introduced Foxglove (*Digitalis*).

It is by no means always easy to determine whether a plant owes its position in the flora of a country to Natural or Human agency. Man was wandering about the face of the globe, transporting plants and seeds to his new homes, long before the existence of botanists and plant collectors. The earliest records of the flora of any country only date back to the 16th century, and these early records of plants were usually extremely incomplete, and often consisted merely in the mention of economic plants, i.e., plants used as food or drugs.

When the early explorers of the world began to visit distant countries (especially new islands), they generally carried with them quantities of seeds of European vegetables, which, together with any impurities such as weed-seeds, they planted liberally on any newly-discovered land. They also took with them sheep and goats and other domestic animals, to turn on to the new lands, and in the fur or wool of these animals there may have been burrs or adhesive fruits of European weeds; and further fodder brought for the animals, perhaps thrown out on the shores, must have contained seeds, while other seeds were probably contained in their viscera, and evacuated by the animals on landing. Again, fruits and seeds sometimes attached themselves to the baggage, gunny bags, packing, etc., thrown on shore, became detached, and an exotic flora was started. A few years later, when collected by an early botanist, the flora thus started was believed to be indigenous, as was the case in *Aristida ascensionis* in Ascension Island.

But long before the 16th century man had been diffusing plants accidentally

or intentionally all over the globe. In every part of the world where human beings have been, some plants have probably been transported with them, at least as soon as agriculture had taken the place of hunting as a means of subsistence. The wild tribes of the interior of the Malay Peninsula (Sakais) seldom cultivate anything, but I have found in the Pahang forests, far from any cultivation, *Colocasia antiquorum* (cultivated in the lowlands, and probably of Polynesian origin), *Pogostemon Heyneanus*, of Indian origin, and *Clerodendron paniculatum*, a favourite plant with the Sakai girls, who gather pieces of the scarlet panicles to decorate their hair, and plant them near their temporary camps. All these plants were growing together, having been carried from afar by these wild folk. It is possible that Palaeolithic hunters may have introduced plants from Africa, or from farther Europe into England, during their chase or in following up the game which abounded in the north, but it is certain that the Neolithic man, with his agriculture, brought in Asiatic plants with his flax and corn seed. Clement Reid shows this in his "Origin of the British Flora." He mentions as plants of Neolithic date only, *Papaver somniferum*, *Fumaria officinalis*, *Lychnis alba*, *Stellaria uliginosa*, *Spergula arvensis*, *Linum* sp. ("Capsules and seeds of flax are so common at Redhall as to suggest that bundles "of the plant were steeped there. Flax is known to have been cultivated in "Neolithic times"), *Prunus domesticus*, *Pyrus aucuparia*, *P. communis*, *Galium palustre*, *Bidens cernua*, *Chrysanthemum segetum*, *Matricaria inodora* (only associated with weeds of cultivation), *Senecio sylvaticus*, *Carduus crispus*, *Centaurea cyanus* (with weeds of cultivation and flax seeds), *Crepis virens*, *Sonchus arvensis* (no other *Sonchi*), *Pedicularis palustris*, *Galeopsis Tetrahit* ("associated with reindeer, "bison and *Bos longifrons*, but not with extinct mammals, suggests a transition "period between Palaeolithic and Neolithic"), *Polygonum hydropiper*, *P. lapathifolium*, *Euphorbia helioscopia*, *Carex canescens*, *C. flava*. A few of these may have occurred earlier, but have not been preserved, but most of them are clearly weeds brought in by Neolithic agriculturalists.

Other plants, such as the red poppies, do not appear till Roman times.

There are comparatively few spots in the world of which the botany has been investigated before the arrival of man, so that it is by no means easy to be always sure whether certain plants (often of wide distribution) are natives, or whether they have found their way there by human agency—at least, in the first instance. In large areas in which only a few wandering hunting tribes live, as in the interior of the Malay Peninsula, very few, if any, exotic plants occur; but as soon as these people begin to clear the ground and cultivate, if only a little tapioca, we find a few alien plants brought with the tapioca, or on clothes or bags, in the form of seeds, round the encampments. These tribes, known as Sakai, occasionally go down to the opened-up districts for tobacco, salt, etc., and accidentally bring on their clothing, etc., seeds of such plants as adhesive-fruited *Bidens pilosa* and *Paspalum conjugatum*, so that we find these round their encampments; but in most cases, as they constantly shift their abodes, the forest grows over an abandoned camp, and the aliens from the open country are shaded out by the forest growth, and disappear again. Thus we have a very large forest area which at present contains nothing but really indigenous plants, or if there are a few introduced ones, they are readily distinguished as aliens. The plateau of Gunong Tahan, in the interior of Pahang, however, first visited by H. C. Robinson in 1905, the Sakais had never been able to reach, on account of the precipitous nature of the surrounding country, and even none of the larger mammals, elephants or rhinoceros, had been able to enter. Only the wild goat (*Nemorrhaedus*) could get in. So here was a locality where no man had ever set foot, and no alien plants could have arrived by human agency; but at a later visit I found that the very first invasion of man had brought the Bracken (*Pteris aquilina*),

as I have elsewhere described. Most of the oceanic islands have been visited very early by man, as I have elsewhere shown in the case of St. Helena and Ascension; and even where the explorers did not leave vegetable seeds, and the weed-seeds, which often accompany them, whalers, pirates, and such people often visited the islands, and very probably accidentally transported alien seeds. Wrecks, too, may have been the source of some invasions of seed, but this does not appear to have been often the case, though they not rarely brought rats to the islands. A few islands, however, appear never to have been visited by man before the visit of the botanists who made complete researches into the flora. In the larger islands, like New Zealand and Australia, although there were botanists on board the discoverers' ships, they had but little time for collecting, and were unable to penetrate very far inland. Their collections were invaluable as far as they went, but usually the discoveries were quickly followed up by settlers, or distributors of vegetable seed, and domestic animals, and it was some years later the botanist came and made a complete collection of all he could get.

The most important islands surveyed by botanists before man had interfered with Nature were Christmas Island, south of Java, and the Island of Krakatau. Christmas Island was visited by Dampier in March, 1688, but he did not land on it on account of its difficult access. Maclear, in H.M.S. "Flying Fish," landed in 1886 and collected a few plants, and Lister, in the "Egeria," in 1887 also collected plants near the coast.

"As previously no settlement had been made on the island, nor any ships "but a few whalers and other ships touched there, the flora was in its primitive "unaltered state, and no weeds of cultivation had made their appearance." In November, 1888, Mr. G. Clunies Ross settled there, and from this period dates the invasion of the weeds and plants generally introduced by human agency. I visited the island in 1890, and was able to collect for about 10 hours, and found a few weeds introduced. Andrews visited it in 1897, at which time one goat only had been introduced.

He made a large collection, which was described in a British Museum volume, "Monograph of Christmas Island." I visited the island again in 1904, and remained for a month collecting every plant I could find, so that we have a regular record of the gradual appearance of the weeds brought by man:—

Up to 1888	No weeds.
Ross settled there, 1888	
My first visit, 1890	4 weeds.
Andrews collects, 1897	12 ,,
Cattle now introduced.	
My second visit, 1904	30 ,,

These weeds grew all round the Settlement and along the paths made through the woods, where men, cattle, and ponies habitually walked. Of these aliens, 2 or 3 had adhesive fruits, 3, *Melia*, *Capsicum* and *Carica*, had been intentionally introduced in 1888, and were being spread by birds and bats, having eatable fruits; the rest were evidently introduced in cattle fodder, vegetable seed, or pot plants. The little nettle *Fleurya aestuans* was found on the island by Lister before any man had previously landed, so that it must have been brought by some bird, the utricles being adhesive; but I observed that we found it not only in the bay where it was first found, but here and there along the coast, wherever fishermen had gone to fish, evidently carried by them on their clothes.

The Island of Krakatau was entirely denuded of vegetation by an eruption in 1883, all plants and seeds apparently being destroyed and covered with hot

volcanic ash. The Dutch visited it on four occasions after this—in 1886, 1897, 1906, and 1919—and kept complete records of the plants as they appeared on each of these occasions. Except for these botanical expeditions, no one visited the island but a European, with many coolies, who settled in the north-east of the island in 1917. None of the common weeds usually dispersed by man were recorded till 1919, when *Cyathula prostrata*, *Synedrella nodiflora*, *Eleutheranthera ruderalis* and *Eleusine indica* were found. All these possess adhesive fruits (though *Eleusine* is rather doubtful). The *Cyathula* may have been brought attached to birds, as we know it sometimes is, but all may have been brought by the above-mentioned European and his coolies, or by the *personnel* or baggage of one or other of the expeditions. What makes this latter suggestion more probable is that *Eleutheranthera ruderalis*, a South American weed, is known only in two spots in the Old World, one of which is the Botanic Gardens, Buitenzorg, Java, whence the expeditions started, the other being the Gardens of Singapore. If this weed came in expedition baggage, it shows again how persistently plants (especially those with adhesive fruits) follow man wherever he goes. A parallel to this is the importation of *Pteris aquilina* to the plateau of Gunong Tahan, in Pahang, twice, by expeditions, mentioned on page 554.

It is, however, not only the migrations of Europeans that we have to look to for alterations of the floras of the different parts of the world. It is quite clear that the Malays travelled to North Australia and even Polynesia long before Europeans knew of the existence of these countries. The coco-nut, as has been shown, travelled with man, as well as by sea, from South America to Asia long before we in Europe knew of the American Continent. There was a constant sea traffic between farthest Asia and Europe in Roman times, and probably before that. The Polynesians invaded New Zealand at a very early date. Indeed, we may say that man has been wandering over the face of the earth ever since he was evolved, and has almost always transported plants intentionally as food or drugs, or accidentally from one place to another for thousands of years.

All migrating or wandering tribes carried some plants about with them, and many cultivated plants, whose history is lost, were doubtless transferred from one country to another by natives long before the times when records were kept. Among these, the Polynesian weeds are perhaps the most interesting. Cheeseman states that the Polynesians were great agriculturists, and that they carried useful plants (and, doubtless accidentally, useless weeds) about to the different islands, including New Zealand; Guppy has studied the Polynesian weeds also with much care, and given a list of 37 species of plants which were found by Cook's botanists, Banks and Solander, the Forsters, and others, who visited the islands before any other Europeans, and investigated the flora (1768 to 1780). All but two of these plants, which he classes as weeds, are of Malay affinities, or, at least, occur in that region, though most are now to be found in the American Continent. He points out, as others have done, that the plants supplying food to the islanders are chiefly of Malay origin: Breadfruit (*Artocarpus*), Bananas (*Musa*), Taro (*Colocasia*), Yams (*Dioscorea*), *Amaranthus melancholicus*, *Dolichos Lab-lab*, and I should be inclined to add *Solanum nigrum*, which all over the East, so far as I have seen, only accompanies man, and is found only in cultivated ground, where, if it is not cultivated, at least it is eaten as a pot-herb. Of the other plants which he classes as weeds, *Geophila reniformis* and *Physalis angulata* are doubtless bird-dispersed, *Sida rhombifolia*, *Urena lobata*, *Bidens pilosa*, *Sonchus asper*, *Adenostemma viscosum*, *Achyranthes aspera*, *Leucas decemdentata*, *Amaranthus caudatus* and *Fleurya interrupta*, are provided with adhesive apparatus, and nearly all are closely associated with man, and carried about by him attached to clothes and bags. *Leucas* and

Fleurya are known to be carried by birds, the fruits adhering (as is probable in all other cases) to the feathers.

Of *Oldenlandia* (2 species), *Hydrocotyle asiatica*, *Vandellia crustacea*, *Cardamine sarmentosa*, the seeds may have been carried on the feet of birds, as we know some of them are; *Cardiospermum*, the 2 *Ipomoeas*, and perhaps *Cassia sophora*, by sea transport.

Oxalis corniculata and *Eleusine indica* were probably accidentally brought somehow by man, as they always appear to accompany him.

Two species he mentions are seemingly exclusively American—*Waltheria americana* and *Teucrium inflatum*. The first of these is now widely spread over the world, but not exclusively by man. Guppy has found its small seeds in the crop of a dove, and I found a distinct species (possibly descended from *W. americana*) on the sandy shores of the Malay Peninsula, which certainly could not have come there by human agency. The plant, however, is not characteristic of oceanic islands. The *Teucrium* is remarkable for its calyx closing over the nutlets, and might possibly be sea-borne, but one form (and the plant collected by Forster is this form) has the globose calyx covered with hairs, and seems to be adhesive, and might be bird-carried. It is extremely improbable that it owes its transport to the agency of man.

The fact that all the weeds of cultivation, as well as the food plants of the Polynesian Islands, came from Eastern Asia, suggests strongly that there was at one time a migration of the inhabitants from the Malayan region to Polynesia. We have evidence that the Malays reached North Australia before the island was discovered by Europeans, and there is no reason why they should not have gone farther to the Polynesian islands, settled in the nearest one, and gradually spread from one island to another, carrying with them their food plants intentionally and their weed-seeds accidentally. We know, too, that a reverse stream of migration occurred as well. The fact that the common names of seashore plants, and of common objects known to the simple seafarers, travelled from Polynesia to Madagascar and the early migration of the coco-nut from Western America to Africa shows this, and the drifting of canoes apparently from some Polynesian islands to Cocos-Keeling, mentioned under Sea-Dispersal, shows that travel from the East westwards for long distances was not difficult for the sea-island folk. But wherever man travelled, he carried with him both useful and useless plants centuries before we have any historical records of his travels.

Before the coming of the human race, there were two elements in the transformation of a local flora—one was the change in the environment, climate, soil, etc., of the flora then occupying the soil, and the other the action of water, wind, and animals in bringing seeds to the spot. When man began to change the flora of a country, he began by altering the environment of the plants he already found there, by agriculture, road-making, and clearing the ground of its primitive vegetation. This in many cases involved the almost entire extermination of the plants previously occupying the soil, and the complete alteration of the environment. This, as Nature fills up blank spaces with vegetation very speedily, entails an invasion of species which previously were unable to get established in the ground. A plant whose area of occupation is very limited, by an alteration of the environment of that, or of a near-lying area, whether by human action or by natural action, may become extremely abundant and spread over a very large area, and, in fact, from being rare may become very common. Here man has, in this way, often effected a vast change in the flora, exterminating some species and causing rare plants to become common, and common plants rare.

Where a country, which in the early history of man was populated by a few wandering tribes who mostly lived by the chase, has become thickly populated

by an agricultural race, the whole flora becomes modified, and eventually completely altered. The forests are destroyed, and for the lofty trees are substituted herbaceous plants of open country. With the death of the forests perish not only the epiphytic plants growing on the branches, but also all the shade-loving herbaceous vegetation. Even where a population is not excessively large, the habit of the native agriculturist of felling, and then cultivating a small portion of land for a few years, and abandoning it when the crops give a smaller return, and felling and clearing another portion, and in due course moving on again, will eventually destroy almost completely the original flora of a large country. This is the history of the present botanical condition of India, Africa, much of Sumatra, Ceylon, and many other countries. As the country so treated becomes denuded of its original flora, and in many cases with the climate, rainfall, and even the soil entirely altered, plants adapted for the changed conditions invade the devastated area. Here and there in valleys, or on the slopes of mountains too steep for cultivation, may remain portions of the original flora, but the greater part of the country contains nothing but herbs and shrubs which can thrive in such spots, exposed to full sunlight, irregular rains, and constant fires. These plants can only come from areas where the conditions of life are similar to those of the altered area—that is to say, from adjacent natural plains, deserts, seashores, open river banks, or the edges of forests abutting on these localities. It is from such places that all the weeds of cultivation come. Fruit-eating birds, wind, rivers, and floods contribute to the new flora, but very many plants are brought by man himself, either in seed of cultivated plants, or attached to the wool of his sheep or hair of his cattle, or as seeds brought gradually along roads and tracks in the viscera of his domestic animals and dropped by the way, to spring up and be carried further on, and in many other accidental ways. So extensively has this dispersal of weed-seeds been carried on accidentally or purposely by man, that the country of origin of many of the now most abundant plants is altogether obscure. They seem to occur only where ubiquitous man has wandered, and have become only weeds by his house or roads or on his agricultural land.

When plants are introduced into a new country, either accidentally or intentionally, they may entirely fail to acclimatise themselves, or they may gradually or immediately settle down, and form part of the flora of the country, or may last for a few years and then die out. In some cases plants so rapidly establish themselves, and even become so vigorous, that they attain a size and vitality far in excess of anything they attained in their original habitats.

Thus Colenso, in 1840, found an almost impenetrable mass of *Rumex obtusifolius*, 4 to 5 feet high, in the interior of New Zealand, which he discovered was the result of a sale of its seeds by a European to a native as tobacco seed, and later he found an earlier introduction had taken place in 1839 by the same method. The ordinary height of the plant is from 1 to 2 feet. Once thus introduced, it was further spread by the rivers all over the country.

The Watercress (*Nasturtium officinale*), when introduced into New Zealand, attained a size and vigour far greater than in Europe. The rapid and extensive growth of the Canadian Water-weed *Elodea canadensis*, when introduced into Europe, and of *Eichornia crassipes*, of Brazil, when introduced into Australia and the East Indies, were very remarkable. These latter two species were entirely reproduced vegetatively, as only one sex of the first named was introduced, and, as far as is known, the latter seldom, if ever, has been reproduced by seed in the Old World.

In most cases where an introduced plant at first spreads very vigorously in its new home, and appears in great abundance, after a certain period it seems gradually to diminish in number, and eventually to take its position as a part

of the flora on the same level of abundance as most of the other species. This is apparently due in some cases to competition with the surrounding flora, and in others to the action of some enemy, insect or fungus, which, owing to the abundance of its food-supply, becomes sufficiently plentiful to restrict seriously the continuous growth and reproduction of the plant. Thus the *Lantana* (*L. mixta*), introduced as an ornamental plant from America to the Old World tropics, spread in vast abundance all over large areas of tropical Asia, often covering wide patches of ground to the exclusion of everything else. In 1888 it was very prevalent in Singapore, but I found in 1915 that it had become much reduced in numbers, and was comparatively uncommon. On examining plants to discover the cause of this, I found that every one of the young fruits on a whole bush was perforated by a small green bug, and that all these fruits which had been punctured by the insect had withered up and never came to maturity. The *Lantana* fruits are remarkably popular with very many birds, who swallow the small black drupes and disperse the seeds. The plant, owing to the attacks of the bugs, which were very abundant and each of which could destroy a large number of fruits, was unable to continue its former rapid reproduction, and so was reduced in numbers. Eventually the former dense masses of the plant would disappear, and the plants become isolated, when they would be more or less protected from attacks of the insect, which would be less likely to find the plant. The fact that when a species becomes too abundant in any one spot, its enemies, insect or fungus, can become so abundant as to destroy it (a fact well known to cultivators) is one of the reasons why it is essential that plants should be able to disperse their seeds at a considerable distance from each other. I treat of this, however, more fully elsewhere in the general considerations as to the necessity of seed-dispersal.

When a plant has been introduced by man into a new country, should it be able to establish itself, it spreads more or less rapidly by wind, water, or animal transport, according to its original habit. It is noticeable that many of the rapid-spreading plants have creeping or underground stems, though others are annuals or short-lived plants which propagate only by seed.

Henslow had a theory, based on a certain number of facts, that self-fertilising plants are much better favoured for propagation than those which are always, or for the most part, inter-crossed. Certainly many of the plants which he says are regularly self-fertilised are very widely distributed. He instances *Capsella Bursa-Pastoris*, *Stellaria media*, *Galium aparine*, *Solanum nigrum*, and *Polygonum aviculare*, and many of the wind-fertilised grasses are also very widely dispersed. It is true that insect fertilisation of a newly-introduced plant is often a failure at first, even if it has showy flowers. I have often noticed, in the tropics, that newly-introduced plants do not fruit the first year, but later are visited by insects, and the fruit sets. The advantage of the frequently self-fertilised weeds and plants with wind-fertilised flowers is that they can commence to spread at once, whether insects visit them or not, and can be disseminated without their aid. Henslow quotes some instances of rapid spread and vigorous growth of plants introduced into New Zealand, which form an excellent appendage to the accounts of the plants already mentioned.

In a letter to Sir Joseph Hooker (*Journ. Roy. Hort. Soc.*, xxxv, 1910, p. 348, which letter was published by Hooker in *Nat. Hist. Rev.*, 1864, p. 124), W. T. Locke Travers writes from New Zealand: "You would be surprised "at the rapid spread of European and foreign plants in this country. All along "the main lines of road through the plain the Knot-grass (*Polygonum aviculare*), "grows most luxuriantly, the roots sometimes 2 feet in length, and the plants "spreading over an area of from 4 to 5 feet in diameter." (This plant in England is usually but 1 foot across at the most.) Kirk, from the wide distance that

this plant has spread in New Zealand, was inclined to believe it to be indigenous, but I imagine that Travers is correct in placing it as an introduction from Europe.

"The Dock (*Rumex crispus*) is to be found in every river-bed, extending 'into the valleys of the mountain rivers until these become mere torrents. 'The Sow-thistle is spread all over the country, growing luxuriantly up to '6,000 feet. A Watercress (*Nasturtium amphibium*) (probably *N. officinale*), 'increases in our still rivers to such an extent as to threaten to choke them 'altogether—in fact, in the Avon, a still, deep stream running through 'Christchurch, the annual cost of keeping the river free for boat navigation 'and for purposes of drainage exceeds £300. I have measured stems 12 feet 'long and ¾ inch in diameter. In some of the mountains, where the soil is 'loose, the white clover is completely displacing the native grasses, forming 'a close sward."

Mr. Darrens observed that the white clover spread over tracts of peaty soil, which, until invaded, supported a dense and luxuriant growth of the New Zealand flax (*Phormium tenax*), but one of the greatest pests was *Rumex acetosella*, the Sheep-sorrel. This, however, was expelled by the white clover. The latter, notwithstanding its extraordinary vigour, was itself unable to hold its own against the Cat's-ear (*Hypochaeris radicata*), or some similar Composite introduced with grass seeds from England. In Nelson, excellent pastures were wholly destroyed in less than 3 years by this weed, which absolutely displaced every other plant on the ground.

The clover and sheep's-sorrel are both creeping plants—the latter having branching underground rhizomes—and have that advantage in overspreading other plants. Similar cases of extensive growth of introduced plants creeping over others and shading them out with their foliage are those of *Hydrocotyle rotundifolia* and *Hieracium aurantiacum* in North America. Similarly, we have the extensive areas of the Lalang grass (*Imperata cylindrica*), probably a native of Africa, which has been widely carried about by man in the form of packing material. The plumed achenes are distributed by wind, and can fly successfully over sea for as much as 25 miles (to Krakatau), but are stopped by a comparatively low and narrow belt of forest. When well established in open country, it will cover a large area, driving out every other plant. Frequently taking fire from lightning or human action, the foliage is burnt off, and with it perish any other plants which have appeared on the ground; but the rhizomes, 8 to 16 inches underground, are unaffected, and the foliage quickly reappears. After burning, it usually flowers and fruits again. I have seen it thriving in a volcanic fumarole in thick fumes of sulphur, in Java, it being the only plant which could survive such fumes, heat, and steam. Like many of the successful weeds, it has several ways of dispersal, e.g., by human agency in packing material, etc., by wind, and by the seeds—swallowed by cattle in feeding—being passed unharmed. *Imperata exaltata* is by no means so abundant a species. It is taller, with a larger panicle, but it grows sporadically. Its rhizome is shorter, consequently it is not liable to form large masses to the exclusion of all other plants, and thus has not the advantage of fires, nor of dispersal as a packing material.

In dealing with the distribution of plants, there are cases which are rather puzzling, their presence in certain localities being unexpected and very difficult to account for, and though it is not advisable to press the possibility of human agency too far, it must be always taken into account *as* a possibility.

The appearance of very fine and abundant plants of *Rumex obtusifolius* in the middle of New Zealand, and the conveyance of *Emex spinosa* from South Africa to Australia by a settler who thought it would make a good pot-herb, have already been mentioned.

Forbes (in "A Naturalist's Wanderings," p. 440) describes the finding of

the French marigold in the middle of Timor thus :—" The sides of the ravine, " however, were covered with vegetation and bright with *Hedychium*, balsams, " and the French Marigold (*Tagetes patula*), so common in our gardens at home, " was here growing wild far from the coast influence or the highways of the " world, and was seen by me nowhere else along my route." It is a widespread plant hailing from Mexico originally, and also found in Africa, but how did it reach the interior of Timor?

Plants introduced by man into a new country are not necessarily those of neighbouring regions, as are those migrating by natural methods, but the travelling flora depends on the origin of and the route taken by their introducers.

Many plants travelled from the north temperate region through the tropics to the Antarctic area, but though plants and seeds could traverse the hot countries, they failed to establish themselves on the way, and only did so when they arrived in a region where the climate and environment were similar to that from which they started from.

In Dunn's " Alien Flora of Britain," excluding plants whose origin is doubtful, and those in which but a single specimen has appeared, and trees which have been planted in parks and woods, I find that, of British aliens, Europe has supplied 540, temperate Asia 68, Africa 4, North America 88, and Australia 4.

In North America the greater number of aliens came from Europe, as is also the case in Australia and New Zealand, the plants accompanying the travellers who went to settle in those countries. In all cases the appearance of aliens was very rapid. Practically nearly all the plants came with the first settlers. We have very little information, however, as to the migrations to North America, as there was a great invasion of settlers before any records of plants were made, though we have one record as early as the 17th century.

The earliest record I have is dated 1672, when John Josselyn published a work called " New England Rarities," in which he gave a short list of " such " plants as have sprung up since the English planted and kept cattle there." He gives only the English names, to which I have added the scientific ones. He mentions Couch-grass (*Agropyrum repens*), Shepherd's Purse (*Capsella Bursa-pastoris*), Dandelion (*Taraxacum dens-leonis*), Groundsel (*Senecio vulgaris*), Pig-weed (*Chenopodium album*), Dog-fennel (*Anthemis cotula*) and Burdock (*Arctium Lappa*). Many of these were doubtless brought in cattle fodder, and the Burdock may also have been brought adhering to sheep's wool, or possibly intentionally introduced as a drug. It may be presumed that none of these plants had been met with in the country before the English settled there.

In tropical Asia the greater number of aliens is derived from South America and the West Indies. As soon as America was opened up, the Jesuit missionaries carried many useful plants of this country to their Settlements at Manila, and thence to Goa and Malacca, and wherever they fixed their missionary establishments, and thence the plants spread to the neighbouring countries, and to the islands, often carried there by natives. Many were useful plants—*Papaya*, *Capsicum*, *Anona*, Pineapple. Others were the usual concomitant weeds, small *Compositae* and grasses, small *Leguminosae*, *Malvaceae* and *Scrophularineae*, brought accidentally in luggage, ballast, or some such way. The Sensitive Plant (*Mimosa pudica*) seems to have been brought as a curiosity.

We have, however, little information as to when and how some of these South American plants first appeared, as the early records of Linschoten, Garcia da Orta, and others, chiefly give lists or accounts of the bringing of useful plants, fruits, drugs, and spices; but it seems probable that most of the American plants in tropical Asia arrived in the 16th and early 17th centuries, and the migration largely ceased with the formation of settlements by the Jesuits. Later, in Java, came the introduction of European weeds in the mountains,

where European vegetables are cultivated, but these have not spread much farther.

In the Equatorial region of Asia the ground was formerly covered with a dense forest, where no herbaceous plants of this type would grow, so that when the forests were felled and burnt, and roads made, there were no indigenous herbs or shrublets of a drier and sunnier habit to take the place of the lost vegetation, nothing except the weedy plants of Brazil and the West Indies, which had been imported, and these plants soon occupied the ground. So that, when I was in Ceylon in 1888, I found that I had to go a long way from Peradeniya, where I was staying, to see any of the native plants of the country, the greater part of the surrounding vegetation being aliens of South America and the West Indies.

Singapore Island was entirely covered with dense trackless forest when Raffles took it over in 1822. This forest was nearly all destroyed by cultivation some years later, and hardly any was left when I arrived in 1888. I found that of the Malay Peninsula aliens, 39 came from South America and the West Indies, 19 from other parts of Tropical Asia, 3 from China, 7 from Africa, 4 from Europe, and 14 were tropical weeds now so widely distributed that their home of origin is uncertain. Out of 37 *Compositae*, 27 species were introduced, and out of grasses (excluding Bamboos) an almost equally large proportion were certainly brought by human agency, and the introduced aliens are now the most abundant and common species, the indigenous plants being more local and scarce.

Tropical Africa, though actually nearer to South America than the East Indies, is at present stocked with a much smaller alien flora, as European colonisation has not as yet progressed very far there. In temperate South Africa, however, there is a large array of aliens from Europe and Asia. Australia and New Zealand have been stocked mainly with aliens from Europe, brought by European settlers at the end of the 18th and 19th centuries. Even when Robert Brown made his collections (the first extensive ones) in 1802, there were a number of European aliens already established in Australia. In Victoria, Ewart gives the following as the origin of the alien flora: from Europe 57 species, from North America 18 species, South America 12 species, North and Central Africa 11 species, South Africa 29 species, Asia 2 species.

It is not only due to the highly-civilised Europeans that plants have been transported from one country to another even across the seas. Allusion has already been made to the importation of alien plants by Neolithic man and by the Persian invaders of Greece. The travels of the Coco-nut Palm from Central America to tropical Asia, carried as it was by Polynesians, Malays, and other tribes, is described under the account of the plant in Sea-Dispersed Plants.

METHODS BY WHICH ALIEN PLANTS ARE COMMONLY INTRODUCED BY MAN.

Among the common methods of introduction of alien plants into foreign countries, we find that the greatest number have been transported in cereals and vegetable seed, in the wool of sheep and hair of cattle, and in their excreta and fodder, in ballast for ships in olden days, and in packing material. A number have also been introduced as ornamental plants or drugs, and seeds accidentally in the mud attached to their roots, in food for fowls and cage-birds, and in many other ways. In some cases they have been introduced so long ago that we really have no definite evidence as to how they arrived at their destination.

We know, however, that plants which can only grow on artificial soil, such as roadsides or arable land, gardens and village sites, could not have

been growing there when the whole country was covered with forests, nor on land reclaimed from the sea, and that if such plants do not otherwise occur in the neighbouring lands, near enough for the seeds to have been brought by wind, water, or animals, they must have been introduced accidentally or purposely by man.

Of the methods of introduction, or spread of plants due to man, I have already treated of some under various sections. Plants disseminated by the adhesion of their burrs to cloth, or wool of sheep, or hair of cattle, or by viscidity to man's clothing or the coats or feet of his domestic animals (all of which were, or could have been, spread by the wild animals which preceded the era of flocks and herds), are dealt with under the sections dealing with Adhesiveness of Fruits and Seeds, p. 532, and the Attachment of Seeds to Human Feet, p. 533, and those of the domestic animals are also treated of in the same section. Transport of seeds by cattle and by man feeding on the fruits and evacuating the seeds, is described in the section dealing with that method of dispersal by animals, p. 340. The present section deals rather with the *mechanical* methods of dispersal, alluded to above.

Dispersal of Weeds in Cereals and Vegetable Seeds.

At the present day seeds of cereals or grass or vegetables are frequently sent out by dealers, with which are mixed the seeds of such weeds as were growing among the crop, and it is extremely improbable that the seeds exported by early explorers were cleaner of weed-seeds than those of the present day. The first thing that a 16th century explorer did, after he discovered a new island or continent, was to visit it again with a large quantity of vegetable seed, together with some domestic animals, such as goats and pigs, plant the seed and release the animals, so that, on later visits, he and others might be certain of finding a supply of food. Thus Capt. Cook, having discovered New Zealand in 1769, returned in 1773 and sowed European vegetables, consisting of cabbage, onions, parsley, carrots, turnips, parsnips and mustard, *Brassica alba* and Purslane, *Portulaca oleracea*, some of which are known to have survived. Crozet, in 1772, planted all sorts of vegetables, pips, and grains there, the seeds of which he brought from the Cape of Good Hope. De Surville visited the island in 1772, and spent three weeks there, and Capt. Marion de Fresne is said to have introduced *Allium vineale* as an eatable onion.

The number of seeds of herbaceous plants carried about and planted with grain and other cultural plants is very large. Even in modern days, when seed dealers are more particular about the cleanness of seeds they export, a large number of weed-seeds accompany them, and there is a greater danger of this occurring when natives and careless dealers export seeds. The danger was no less in the early days, when explorers carried vegetable seed to remote parts of the world and broadcasted them in the vicinity of their landing-place, ostensibly for the use of future travellers.

Thomson writes that he imported into New Zealand grass seed from a good dealer in Edinburgh, in 1870. These seeds were those of various grasses, *Lotus*, *Medicago*, and *Trifolium*. With them came *Chrysanthemum leucanthemum*, *C. segetum*, *Lychnis Githago*, *Geranium molle*, *Ononis arvensis*, *Anthyllis vulneraria*, *Vicia sativa*, *Scabiosa arvensis*, *Taraxacum dens-leonis*, *Prunella vulgaris*, *Veronica Chamaedrys*, *Cuscuta trifolii*, *Sinapis arvensis*, *Papaver Argemone* and *Papaver Rheas*.

In Dunn's "Alien Flora of Great Britain" a very large proportion of the introduced weeds are recorded to have appeared in spots where grain-siftings have been strewed.

Druce (in the *Botanical Exchange Club Report*, 1926) records the following from maltings in Burton-on-Trent:—*Sisymbrium altissimum*, *S. orientale*, *Medicago falcata*, *Melilotus arvensis*, *Lathyrus tuberosus*, *Xanthium spinosum*, *Centaurea melitensis*, *Echinospermum lappula*, *Chenopodium murale*, *C. opulifolium*, *C. leptophyllum*, *C. glaucum*, *Asphodelus fistulosus*, *Setaria glauca*, *Polypogon monspeliensis*, *Festuca ligustica*, *Bromus rigens*, *B. tectorum*, *B. rubens*, *B. arvensis*. *Asphodelus fistulosus* is also recorded by Maiden, as carried about in wheat grain in Australia.

Here the seeds were, no doubt, brought in the barley for malting, and thrown out of the works. Frequently the barley or other grain is sown in cornfields, and with it grow the weed-seeds. Most of our annual cornfield weeds, originally from Eastern Europe and the Asiatic borderland, were introduced in weed and vegetable seed, and in this way were also carried to North America, temperate South America, Australia and New Zealand. In fact, the largest number of aliens in Dunn's "Alien Flora of Britain" have apparently been introduced in Turkish barley and such-like grain. Indeed, most of the British aliens have been introduced from temperate Asia, though some have arrived from North America.

George Stewart (in "Alfalfa-growing in the United States of America and Canada," 1926) records that it is not infrequent in Alfalfa seed (*Medicago sativa*) to find 400 weed-seeds in the ounce, giving for 15 pounds of seed to the acre, no less than 96,000 weed-seeds. These include *Cuscuta*, *Setaria*, *Salsola*, *Rumex* and *Medicago lupulina*, while *Centaurea picris* occurs in seed from Turkestan.

In "Poisonous Plants and Naturalised Aliens of Victoria," A. J. Ewart records the following plants as introduced in agricultural seed:—*Diplotaxis tenuifolia*, *Lepidium Draba*, *Silene inflata*, *Lychnis Githago*, *L. diurna* (*dioica*), *L. vespertina* (*alba*), *Saponaria officinalis*, *S. vaccaria*, *Sherardia arvensis*, *Galium aparine*, *Arctium Lappa*, *Verbascum blattaria*, *Lithospermum arvense*, *Polygonum convolvulus*, *Chenopodium ambrosioides*.

In the "Alien Plants of Essex" (*Essex Naturalist*, xxii, 31, 1927) G. C. Brown gives as introduced plants growing on malt refuse the following:—*Hypecoum pendulum*, *Fumaria parviflora*, *Sisymbrium orientale*, *Brassica napus*, *B. juncea*, *Carrichtera Vellae*, *Lepidium sativum*, *L. neglectum*, *Vogelia paniculata*, *Rapistrum rugosum*, *R. Linneanum*, *Erucaria myagroides*, *Raphanus sativus*, *Saponaria vaccaria*, *Silene angustifolia*, *Malva parviflora*, *Medicago falcata*, *M. sativa*, *M. scutellata*, *M. tribuloides*, *M. tuberculata*, *M. turbinata*, *M. hispida*, *M. laciniata*, *Melilotus sulcata*, *M. arvensis*, *M. indica*, *Trifolium incarnatum*, *T. stellatum*, *T. tomentosum*, *Astragalus boeticus*, *Hosackia americana*, *Coronilla scorpioides*, *Vicia calcarata*, *V. bithynica*, *V. narbonensis*, *V. lutea*, *V. pannonica*, *V. peregrina*, *Lathyrus cicera*, *L. hierosolymitanus*, *L. ochrus*, *L. aphaca*, *Pisum humile*, *Epilobium humile* (from Chile), *Bupleurum rotundifolium*, *Peucedanum sativum*, *Caucalis leptophylla*, *C. daucoides*, *Galium tricorne*, *Asperula arvensis*, *Xanthium strumarium*, *X. spinosum*, *Madia sativa*, *Hemizonia pungens* (these four American), *Anthemis arvensis*, *A. Wiedmannianus*, *A. muricata*, *Chrysanthemum coronarium*, *Calendula arvensis*, *Carduus solstitialis*, *C. melitensis*, *C. pallescens*, *Rhagadiolus edulis*, *Lactuca scariola*, *Anagallis femina* (*A. coerulea*), *Gilia squarrosa*, *Amsinckia Menziesii* (American), *Hyoscyamus niger*, *Antirrhinum majus*, *A. orontium*, *Plantago indica*, *Pl. lagopus*, *Amaranthus retroflexus*, *Chenopodium murale*, *C. vulvaria*, *Beta vulgaris*, *Rumex salicifolius*, *Emex spinosa* (South Africa), *Panicum miliaceum* (Asia), *Phalaris minor*, *P. paradoxa*, *Polypogon monspeliensis*, *P. maritimus*, *Avena fatua*, *A. sterilis*, *A. sativa*, *Bromus rigens*, *B. squarrosus*, *Lolium temulentum*, *L. multiflorum*, *Triticum turgidum*, *Hordeum hexastichon*.

This list gives a very good idea of the large quantity of different seeds of alien plants dispersed in grain. Most of them are European, chiefly Mediterranean, a few are American. They belong to a number of orders, *Leguminosae*,

Cruciferae, and *Compositae* being most abundant. Many other lists of grain and vegetable alien seeds occurring in different parts of the temperate regions, which would be too extensive to give here, have been published in other works. Some of the plants are quite dwarf, *Fumaria*, *Anagallis*, etc., but most are fairly tall, and would very readily be taken up in cutting the wheat and barley, and their seeds mixed with the grain. Some are now very widely spread over the world; others, more scarce, are still continuing their migrations.

T. Johnson and Miss R. Hensman also give an account of the weed-seeds introduced in cereals in agricultural seeds and weed impurities (in *Sci. Proc., Roy. Soc., Dublin*, vol. xii, July, 1910, p. 446), showing the great amount of weeds so introduced.

In the "Naturalised Flora of South Australia" J. M. Black records 368 species, of which 220 are European in origin, including the Mediterranean region; 60 he classes as cosmopolitan, 10 Asiatic, 44 South African, 1 Abyssinian, 2 from the Canary Islands, 9 North American and Mexican, and 15 South American. The remainder were imported from other parts of Australia.

This transportation of weed-seeds in cereals and crop grain has been continuous for a vast number of years—indeed, as long as any cultivation of cereals has taken place. I have already mentioned the importation into Europe of the seeds of many weeds with corn and flax in Neolithic times. Whether the cultivations were of wheat, barley, rye, flax or rice, wherever these plants have been grown, weeds have grown with them. If the fields are abandoned, many of the weeds persist. The cereal, when carried home for food, is cleaned of the weed-seed, which is thrown away on waste ground or on roadsides. It is fed to cattle and horses, and the seed often passes through them, unharmed, far away from the cultivation area, or it is spilled from the food-bags on the roadsides, thrown out in maltings, fed to fowls, or dropped from the bags at the docks. In these and numerous other ways the seeds of small herbaceous plants are strewn about everywhere, and should any of them alight upon a spot suited for their growth and reproduction, they may eventually form a part of the flora, and become cosmopolitan, or wide or common plants.

Vegetable Seeds.—These often contain impurities in the form of weed-seeds which are accidentally sown with them. I have on more than one occasion seen plants of *Asphodelus fistulosus* coming up with onions in England. The onion seed had been imported from Italy, and the seeds of the Asphodel (a native of the Mediterranean region), which much resemble onion seed, had been accidentally gathered with it, and was actually sown in the same hole with it, so that the two plants came up together.

In the Tosari district of Java the hills are terraced and put under a very extensive cultivation of European vegetables. The original hill-forest which formerly covered this area has been so largely destroyed that the inhabitants have to build their houses of split bamboos for lack of wood. A few trees remain here and there in gardens, some relics of the lost forest, others introduced, such as the peach and Spanish chestnut, otherwise trees are absent. The most conspicuous plants on these hillsides are a fine form of the Radish (*Raphanus sativus*) and a shrubby *Datura* from South America (*D. arborea*). The banks of the waysides and the waste ground are covered with a vegetation composed of a mixture of European weeds and the original herbaceous flora of the Java mountains. The European plants were undoubtedly introduced, as impurities, at some time with the vegetable seeds. Among them are the following plants:—*Cardamine hirsuta*, *Capsella Bursa-Pastoris*, *Brassica juncea*, *B. campestris*, *Barbarea vulgaris*, *Fumaria officinalis*, *F. parviflora*, *Cerastium triviale*, *Spergula arvensis*, *Stellaria media*, *Trifolium procumbens*, *Torilis anthriscus*, *Coriandrum sativum*, *Foeniculum vulgare*, *Senecio vulgaris*, *Poa annua*, *Dactylis glomerata*, and *Briza minor*.

Most of these European weeds I found there myself. The Groundsel (*Senecio vulgaris*) was rather remarkable. I found a small field so thickly covered with it that it was quite yellow. Usually, in England, it grows sporadically, but there it was in mass.

In Sumatra, at Berastagi, potatoes are cultivated extensively, and a good many weeds, such as *Salvia plebeia*, *Plantago major*, *Torilis anthriscus*, and *Poa annua*, are to be found in the potato plots. In this case the seeds may have been brought in mud on the potatoes, as I believe many weeds are carried from one place to another in the mud on tapioca roots in the East Indies.

Lyster D. Dewey states that *Cyperus rotundus* was introduced into Arkansas with strawberry roots, and into California with orange trees from Florida; *Allium vineale* in lawn grass seeds and among the bulbs of Grape-hyacinths (*Muscari*). It was also said to have been introduced into Pennsylvania as a flavouring agent, as it was by De Fresne into New Zealand. The *Cyperus* has subterranean tubers by which it is very readily reproduced, and is very troublesome to eradicate, as digging it up serves simply to diffuse the tubers and aid in its propagation. Hence it has been called "Hydra-grass." It occurs all over the warmer parts of the globe, but mainly in cultivated ground—at least, in tropical Asia. Its home of origin is quite obscure.

Allium vineale reproduces itself largely from bulbils in the flower-head, which replace the flowers. The plant, common as it is in Europe, is apparently of slow dispersal without the aid of man, as the bulbils sink in water, and are only dispersed by wind shaking the head, and by rain-wash. Marquand found two plants of it in Guernsey at a spot by the Grand Mare, in 1890, and I found it in the same spot, and nowhere else, in 1924 and 1925, a single clump. It is curious how common this form is (var. *compactum*) which produces bulbils only, compared with the flowering form, which is quite rare.

In Bird Food.—A large number of plants have been diffused over the world in seed for feeding poultry and cage birds. The grain thrown down near poultry runs and the sweepings of bird-cages ejected on to rubbish heaps, account for the presence of a certain number of plants in various countries. The transport of poultry to different parts of the world was commenced very early. According to Heyn, the domestic fowl was first brought to the West from Asia by the Medo-Persian invaders 424 B.C., and is mentioned by Theognis and Aristophanes between 400 and 500 B.C.; but Darwin states it is figured on Babylonian cylinders between the 6th and 7th centuries B.C., and on the Harpy tomb in Lycia in 600 B.C. It is reported in China 1400 B.C. The fowls were always carried about on ships by early explorers, and often turned loose on the newly-discovered islands, and with them corn and rice containing weed-seeds for their food. Singing birds have also been carried about the world for very many centuries on ships, and with them there would be carried bird seed.

Nowadays chickens are largely fed on the screenings and waste from grain stores, which is thrown down in and round the poultry runs. Many seeds escape being eaten by the birds, or are rejected by them, and germinate and grow. Miss M. C. Knowles (in a contribution to the "Alien Flora of Ireland," *Irish Naturalist*, 1906, xv, 143) gives an account of finding on a piece of waste land a number of aliens, including *Lepidium campestre*, *Thlaspi arvense*, *Silene noctiflora*, *Medicago denticulata*, *Malva* of several species, and *Amsinckia lycopsioides*. The ground proved to be the site of an abandoned cottage, where a clerk of the Lyons wheat mills had formerly resided and kept fowls, feeding them from the screenings and dirty stuff from the mills.

The wheat had been derived from India, Russia, Australia, and North America. The authoress gives a list of the plants found about the chicken runs and the mills, of which 6 came from Central Asia, 10 from Northern Europe, 15 from North America, and 28 from South-East Europe and Western

Asia. The mill owner stated that the dirtiest wheat came from the Caspian region, and the cleanest from Australia. It will be noticed that the largest number of weeds were natives of South Europe and Western Asia.

T. Johnson and Miss Hensman (in "Agricultural Weeds and Impurities") give a list of 112 species from screenings found in Ireland. They note that indigenous Australian and New Zealand plants adapt themselves badly for cultivation, but European weeds brought from those countries, where they had been introduced, thrive. One of the most common chicken and bird food aliens in England is *Phalaris canariensis* (canary seed), common on rubbish heaps, where I have found it growing with *Cynosurus echinatus* on the Mortlake rubbish dump. I have also seen plants of *Potentilla norvegica* in chicken runs in Surrey, and *Lychnis Githago*, *Verbascum Thapsus*, *Reseda luteola*, and many other such plants in similar spots in Guernsey. Dunn records *Ranunculus falcatus* as introduced in chicken food, and I have seen plants of *Bromus* sp. and *Fagopyrum* growing where pigeons were fed.

Mr. White Spruner records the following aliens occurring at Greenland, Belfast, which Mr. Lloyd Praeger probably correctly considered were brought in foreign grain and fed to chickens at this spot:—*Sisymbrium Sophia*, *Thlaspi arvense*, *Erysimum orientale*, *Linum perenne*, *Lychnis alba*, *Melilotus alba*, *Cichorium Intybus*, *Hyoscyamus niger*, *Galeopsis speciosa*.

Hyoscyamus niger, the Henbane, is frequently to be found in rubbish heaps and waste ground in England, very probably thrown out with waste from chicken runs, and probably rejected by the fowls.

Chickens are fed on rice in the Asiatic tropics, and are carried about all over the country, even as food, far up into the forests. The impurities of the rice are mostly seeds of swamp plants, but some of the seeds so carried may be dispersed to great distances. A form of *Stellaria uliginosa*, found on banks of the hills of Perak, Malay Peninsula, probably came in Chinese rice, and was perhaps fed to fowls, the nearest locality for the plant being China, where it grows in rice-fields.

Dust Carts, etc.

There are a number of papers and books published on town weeds, the seeds of many of these weeds being carried about by man, and dropped in the streets. Burkill (in "Plants Distributed by Cambridge Dust Carts") gives an extensive list of plants found growing on Coe Fen, where the town dust was deposited. Of these, 58 per cent. were roadside plants, 14 per cent. garden plants, 25 per cent. due to human agency, 3 per cent. of doubtful origin. The human agency plants included horse fodder, chicken, and singing-bird waste seeds. The rubbish heaps of towns and villages often produce numbers of alien plant seeds carried from dustbins in carts.

London Building Sites.

J. C. Shenstone (in the *Journ. Bot.*, vol. 40, p. 117, 1912) gives an account of the flora found on building sites in London. He examined five spots where clearing had been going on, and made a list of the plants found. These spots were Farringdon Street, British Museum, Bloomsbury, Upper Thames Street, Russell Street, Covent Garden, and the corner of St. John's Street, Clerkenwell.

The weeds which came up were numerous, and, except for wind-dispersed plants, must have owed their appearance to man in some way. The wind-dispersed plants were *Epilobium angustifolium* (at all stations), *E. roseum* (at 3 spots), *E. montanum* (1 station), *Tussilago farfara* (all stations), *Erigeron canadense* and *Carduus arvensis* (at 4 stations), *Senecio vulgaris* (3 stations), *S. Jacobaea* (2 stations), and *S. viscosus* (not a common plant round London) (2 stations),

Taraxacum dens-leonis (3 stations), *Sonchus oleraceus* (2 stations), *S. arvensis* (1 station), *Artemisia vulgaris* (1 station), *Achillea millefolium* (1 station), *Lastrea filix mas* (a wind-dispersed garden plant). Under small-seeded plants, which he suggests might be carried on birds' feet, he gives *Capsella Bursa-pastoris*, *Stellaria media*, *Cerastium vulgatum*, *Polygonum aviculare* and *Senebiera*. The first 3 are certainly eaten by horses, and the seeds passed. The dispersal of the last 2 is rather obscure, but I have seen *Senebiera* coming up where horse manure has been thrown. Bird-dispersed, *Sambucus nigra* only.

Forage and Packing.—This includes plants often met with in corn fed to horses, and as then many horses were employed in the work of bringing material, etc., many of these plants were, no doubt, waste grain in the nose-bags supplied to the horses. Some of the plants may have been brought in hay or straw packing.

Plantago major in all localities (this, however, is commonly sold as bird seed, and may be due to the sweeping out of bird-cages ; it is the most abundant plant), *Plantago lanceolata* and *P. media* (1 locality both probably in hay) ; *Silene latifolia* (*S. inflata*) (2 localities), *Lychnis alba* (1 locality), *Melilotus officinalis* (2 localities), *M. alba* (1 locality), *Sisymbrium Irio* (1 locality), *S. officinale* (1 locality), *Thlaspi arvense* (1 locality), *Trifolium repens* (3 localities), *Matricaria inodora* (2 localities), *Chenopodium album* (1 locality), *Atriplex patula* (3 localities), *Rumex crispus* (1 locality), R. *obtusifolium* (2 localities) (these docks probably adhesive to horses' hair), *Polygonum convolvulus* (4 localities), *P. persicaria* (3 localities), *Urtica dioica*, *Poa annua* (4 localities, largely wind-dispersed), *Agrostis alba* (4 localities), *Avena sativa* (4 localities), *Dactylis glomerata*, *Triticum vulgare*, *Hordeum distichum*, *Lolium perenne*, *Poa pratensis* (1 locality each), *Pteris aquilina* (no doubt the spores carried in packing) (3 localities).

Locally Cultivated Plants.—A number of seedlings came up from plants which had probably been planted in gardens, and this was especially the case in the Bloomsbury site, where the author suggests there must have been a botanist's garden, for here were found: *Camelina sativa*, *Berteroa incana*, *Potentilla recta*, *P. intermedia*, *Ampelopsis quinquefolia*, *Oenothera biennis*, *Carthamus tinctorius*, *Artemisia Absinthium*, *Cichorium Intybus*, *Atropa belladonna*, *Polygonum cuspidatum* and *Carduus setosus* (a rare form of *C. arvensis*). Other cultivated plants were *Papaver somniferum*, *Brassica napus*, and *B. oleraceus*, *Sinapis arvensis* (1 locality each), *Raphanus sativus* (3 localities), *Carum petroselinum* (1 locality), *Ficus carica* (2 localities) and *Oxalis acetosella* (1 locality).

The vegetable seeds may have come from a seed shop, the *Oxalis* from a garden.

The absence of *Sagina apetala*, so common in the suburbs and small towns as a wall plant, was probably due to the dryness of the London sites.

Sisymbrium Irio, the London Rocket, has a historical interest, as it is recorded to have appeared in vast abundance 8 months after the Fire of London, 1666. It appears, however, that it was abundant in London and the suburbs on walls before the fire. Baxter says it came up in abundance outside the walls of Oxford Botanic Gardens, on ground where rubbish from the garden had been burnt and trenched, the ashes being spread over the ground ; a large crop came up in 1835—probably from garden plants. The plant is quite scarce in England now.

BALLAST.

Ballast is sand or gravel carried about in ships for the purpose of weighting them. It was formerly much more in use, but of late years water-ballast has replaced it to a large extent. It was usually taken from near the shore whence the ship started, and was discharged at the port of destination. Hence the

seeds or fruits which happened to be lying in the sand or shingle on the shore might be, and often were, transported by ocean travelling ships to great distances, and usually discharged on ground similar to that from which they came.

So noxious were the seeds brought in ballast to New Zealand that at one time the authorities forbade any captain to unload ballast on the shores, and ordered that, unless it consisted of rocks, it should be taken out to sea and discharged there. As, however, many of the seeds could float ashore, this policy was considered of doubtful value. Even if the seeds did not float, they might yet be washed up in sand or silt, unless sunk in very deep water.

Very many plants have thus been carried from one port to another, though perhaps not all the species have travelled in this way which have been supposed to.

Xanthium strumarium and the seeds of 17 other plants, some of which had been previously introduced to New Zealand, were brought in one ship from Buenos Ayres.

J. C. Martindale (*Bot. Gaz.*, ii, 55 and 127) gives an account of the plants introduced in the ballast heaps of Philadelphia, of which I give a selection of the most interesting :—

Ranunculus repens, R. *bulbosus* and R. *philonotis*, *Erysimum cheiranthoides*, *Brassica monensis*, *Diplotaxis tenuifolius* and *muralis*, *Thlaspi arvense*, *Camelina sativa*, *Lepidium ruderale*, *Senebiera coronopus* and *S. didyma*, *Sisymbrium sophia* and *S. irio* (these Crucifers seem to occur in ballast or sweepings from ships, everywhere), *Silene inflata*, *S. noctiflora*, *S. dichotoma*, *Lychnis alba*, *L. dioica*, *Potentilla reptans* and *P. anserina*, *Poterium sanguisorba*, *Reseda luteola*, *Cleome pungens* and *Gynandropsis pentaphylla* (much dispersed by cattle), *Tribulus terrestris*, *Geranium molle*, *Erodium cicutarium*, *Medicago falcata*, *M. sativa* and *M. lupulina Melilotus* (the three common European species), *Lotus corniculatus*, *Lathyrus aphaca*, *Trifolium hybridum* and *Vicia cracca* (the *Geraniaceae* and *Leguminosae* are habitually carried about by cattle swallowing the seeds in fodder, and were probably brought in shipments of cattle), *Vigna glabra*, *Scandix pecten*, *Centaurea Cyanus*, *Carduus pycnocephalus*, *Anthemis nobilis*, *Tussilago farfara*, *Aster flexuosa*, *Solidago sempervirens*, *Acanthospermum xanthioides* (these three last of American origin), *Artemisia absinthium*, *Senecio Jacobaea*, *Centaurea solstitialis*, *Helminthia echioides*, *Picris hieracioides* (these Composites partly in fodder and partly adhesive to animals), *Veronica hederaefolia* and *V. Buxbaumii*, *Linaria spuria*, *L. minor* and *L. Elatine*, *Godetia quadrivulnera* and *Gilia capitata*. adhesive (both from Western America), *Echinosperum lappula*, *E. Redowskii* of America, *Myosotis arvensis*, *Asperugo procumbens*, *Anagallis coerulea*, *Antirrhinum orontium*, *Scoparia flava*, *Lycopus europaeus*, *Plantago coronopus*, *Stachys arvensis* and *S. sylvatica*, *Heliotropium europaeum* and *H. curassavicum*, *Tournefortia heliotropioides*, *Solanum sisymbrifolium*, *Datura metel*, *Nicotiana longiflora*, *Chenopodium polyspermum* and *C. vulvaria*, *Salsola Kali*, *Atriplex arenarius*, *Amaranthus deflexus*, *Polygonum herniarioides*, *Euphorbia* (five or six species), *Carex hirta* and *C. muricata*, *Alopecurus agrestis*, *Agrostis spica-venti*, *Lolium temulentum*, *Holcus mollis*, *Andropogon halepensis*, *Panicum miliaceum*. This list consists chiefly of European plants, many being well-known English ones. The plants in some cases are evidently true ballast plants (*Diplotaxis*, *Salsola*, *Atriplex*, etc.), sea-sand inhabitants which have been conveyed in the sand dug up off the shore. Others are more closely associated with cattle, and brought in fodder, or in their dung, some cornfield weeds probably brought in grain, some adhesive plants brought attached to baggage, to clothes, or to the hair of cattle. In fact, the collection is largely made up of the sweepings and rubbish accidentally brought by ships, as well as the seashore plants.

C. Mohr (in "Plant Life of Alabama," Contrib. U.S.A. Nat. Herb., vi, 1901) mentions, in his list of Alabama plants, a number of aliens introduced

in ballast, and largely confined to the ballast heaps and vicinity of the shipping. I give a list of some of the more interesting of these, as it illustrates from what different parts of the world plants may be introduced in this way :—

From Europe : *Picris pauciflora*, *Sonchus tenerrimus*, *Chrysanthemum segetum*, *Artemisia vulgaris*, *Euphorbia Peplus*, *Mercurialis annua*, *Erodium cicutarium*, *Lotus corniculatus*, *Medicago minima*, *Diplotaxis muralis*, *Brassica nigra*, *Fumaria officinalis* and *F. Vaillantii*, *Ecballium elaterium* (this plant also is found in the Azores : did it arrive there in ballast ?)

From Asia : *Melochia corchorifolia*, *Sida cordifolia*, *S. urens*, *S. acuta*, *S. carpinifolia*, *S. linifolia*, *Phaseolus semierectus*, *Cicer arietinum*, *Crotalaria Brownei*.

From America : *Martynia diandra*, *Momordica charantia*, *Flaveria trinervis*, *Hymenoxys anthemoides*, *Chrysanthemum coronarium*, *Crozophora tinctoria*, *Indigofera miniata* (from Cuba), *Senebiera coronopus*, *Lepidium apetalum*.

Some of the plants I put under Asia are now practically distributed all over the warmer parts of the world, and may have been directly received from the American coasts.

Poterium canadense was found at Arrochar, Loch Long, Scotland, by Canon Little, who states that it is believed to have been brought in ballast. *Salsola Kali* appeared in 1926 on the Thames bank between Kew and Mortlake, in sand and shingle brought by barges from the mouth of the river for enlarging the towing-path. *Polypogon monspeliense* and *P. littoralis* seem to be occasionally brought in ballast. Dunn mentions *Ononis natrix*, *Medicago minima*, *Vicia pseudo-cracca* and *Echinophora spinosa*, as plants introduced in ballast in England.

A. J. Ewart (in "Poisonous Plants and Naturalised Aliens of Victoria," 1909) mentions *Diplotaxis tenuifolia* as introduced in ballast.

In South Australia, J. M. Black ("Naturalised Flora of South Australia") records the occurrence of 268 aliens, including *Glaucium luteum*, *Cakile maritima*, *Plantago coronopus*, *Hordeum maritimum*, all probably introduced in ship's ballast taken in from the coasts of Europe.

Apium leptophyllum is a small weedy herb, native of Texas, Florida, and South America, but now dispersed widely in Europe, West Africa, Mauritius, China, Japan, Australia, New Zealand, and Polynesia. According to Sprague (*Journ. Bot.*, 1893, p. 129), it is disseminated in earth with ship's ballast, pot plants, wool, guano, and among agricultural seeds.

A rather curious history attaches to the South American shrublet *Croton sparsiflorus*. In about the year 1897 a ship arrived at Chittagong from La Plata with ballast of mud from South America. To get rid of the mud, it was supplied to a local gardener for soil. In it were seeds of the *Croton*, which germinated and grew. The plant travelled along the railways, and by steamer to Diamond Harbour, Calcutta (1917), and along the rail-banks to the Botanic Gardens (1926), up to Mushedabad and Dacca. Some years ago it appeared on the West Wharf, Singapore, where the Calcutta steamers unload, and is now spreading over waste ground round the town. Mr. Burkill, who noted its first appearance in Singapore, states that its small oblong seeds became emmeshed in gunny bags, and when these are thrown out at the various ports, the seeds are detached and presently start to grow. An account of its wanderings in India is given by P. Bruhl (in *Journ. As. Soc. Beng.*, iv., n.s., 1908, 603).

Soil Export.—Another method in which seeds may be transported is in soil conveyed from one place to another for the purpose of cultivation. In the Singapore Botanic Gardens we not infrequently shipped soil to Cocos-Keeling Island and to Bangkok, in Siam, for garden purposes, there being in those places no suitable soil for any cultivation. In Cocos the ground was all

coral reef, in Bangkok a stiff clay. I have little doubt that plants were introduced in this way, their seeds lying in the soil. Export in pots of other plants has been mentioned, and undoubtedly some weeds have come from one part of the tropics to another in Wardian cases to botanic gardens, and so escaped. As early as the 14th century Ibu Batuta mentions that the Chinese, travelling between China and India, carried in their junks greenstuff, vegetables, and ginger growing in soil in wooden tanks.

Transport of Road Material.—The conveyance of soil, sand, and railway ballast for making embankments or tracks may be responsible for the diffusion of many species of plants across country.

I have found plants of *Boerhaavia repens* (*Nyctagineae*) growing between the rails on the railway line at Muntilan, in Java, where obviously sand-ballast had been brought from the far-distant seashores, as this plant in the Malay region is only to be found on sand and shingle close to the sea. On a cart-track in the interior of the forest region at Bukit Tanga, in Negri Sembilan, Malay Peninsula, 36 miles from the sea, I found the seashore Convolvulus, *Ipomoea biloba*, growing, and well established, though so far from the sea. Its seeds had clearly been brought by carts in sand from the shore. I have also seen the same plant growing inland on the banks of the railway at Kota Bahru, sea-sand having been used in the making of the raised embankment.

Many of the alien plants found on railway banks in England and elsewhere are doubtless brought from long distances in railway ballast. Druce records finding *Herniaria hirsuta* and *Antirrhinum majus* in sand-ballast at Burton-on-Trent. *Herniaria* is a small tufted plant which grows normally in sea-sand; the seeds do not float, and it is probably frequently transported in sea-sand from one place to another. I have found *Silene italica* at Ham gravel pits, evidently brought in ballast barges.

In America a large number of plants are recorded as having travelled along the railway tracks and banks, probably from the transport of soil for long distances for the construction of the line.

Fodder.—A large number of plants have been widely spread in fodder for horses, cattle, camels, etc. The fodder may be carried in ships or trains to feed animals on their passage, and the seeds and detritus swept out at the landing port, or, in case of long distances—caravans over deserts, etc.—fodder may be carried by the animals themselves. In these ways many grasses and other plants can be widely dispersed.

Grant (in "Speke's and Grant's Travels in Africa," *Linn. Trans.* xxix, 101) records seeing a camel carrying a load of *Centaurea calcitrapa* (*Compositae*), probably for fodder. This plant is widely spread, chiefly by its seeds carried in cereals as well. Grant found it common at Thebes.

Anthistiria cymbaria (*Gramineae*).—This (according to Ferguson in Trimen's "Flora of Ceylon," v, 249) is largely cut and dried for fodder for cattle in Ceylon, and several years ago (dating from 1886) large quantities used to come from Bombay with batches of horses for sale.

Many plants have followed armies of invasion, probably brought in fodder. St. Hilaire states that, after the war of deliverance, in many places where the Cossacks camped was found the Tickseed (*Corispermum Marschalli*), a plant allied to the Goose-foots (*Chenopodium*), and indigenous to the Dnieper steppes; and in a similar manner was *Bunias orientale* spread with the Russian hosts in 1814, through Germany, even to Paris. *Juncus tenuis* is believed to have been introduced into England in American fodder. *Medicago sativa*, the alfalfa or lucerne, is a fodder plant which has been largely transported all over the temperate regions of the world. It is a native of Mesopotamia, Persia, and Siberia, and was introduced, apparently in fodder, to Greece by the invading Medes and Persians about 424 B.C., whence it spread all over Europe, and

later to America. Most of its recent dispersal, however, has been effected by seed intentionally introduced and cultivated.

Proboscidea fragrans was introduced into South Africa in fodder during the Boer War, with mules brought from Texas, according to Burtt-Davy.

Sporobolus indicus, a common East Indian grass, is said to have been introduced into New Zealand in 1840 by S.S. "Soerabaya," with horses and their fodder, the hay largely consisting of this grass.

Hay is, of course, carried about everywhere, and contains a large amount of seed of grasses and herbaceous meadow plants. The hay-carts, when travelling through narrow lanes, often lose wisps of grass and other herbaceous plants, brushed off the waggons as they go along by the hedges, and thus plants may travel for miles, and their seeds be scattered along the roadsides, and the hay even transported for sale to far-distant countries.

Plants Introduced in Packing Material.

A number of plants have been introduced into various localities far distant from their original homes by the seeds being conveyed accidentally in packing material, or by their attachment to bags or baskets in which cargo is packed.

Thus *Chloris barbata* Sw., a grass, probably a native of tropical Africa but now abundant in many parts of India, Ceylon, and South America, apparently owes its wide distribution to this method of travel. In Java and the Malay Peninsula it is quite confined to the neighbourhood of the docks, and is abundant in such spots in Singapore, Johor, and Province Wellesley. The spikelets adhere readily to sacking by their awns.

Imperata cylindrica, the Lalang grass, is often used as a packing material, and there can be little doubt that it owes its very wide dispersal over nearly all warm parts of the world to this use of it.

I have picked up in the streets of Pernambuco, in Brazil, a fruiting spike of one of the African *Pennisetums*, which had been clearly brought in some packing of goods from Africa.

L. Cockayne (in an article on the dispersal of weed-seeds in *New Zealand Journ. Agric.*, 1926, xxxiii, 23) states that the Horned Poppy (*Glaucium luteum*), found now abundantly in sandy soils on the Wellington coast, was introduced in machinery imported for the Patent Slip at Wellington, New Zealand; and the seeds of the Californian Thistle (*Cnicus arvensis*) have been found in the straw wrappers round bottles.

G. F. Marsh (in "Man and Nature," 68, in 1864) says that *Erigeron canadense* was introduced into Europe 200 years ago, in the filling of a stuffed bird; and Vaupell states that when Thorwaldsen's treasures were brought from Italy, and unpacked in the court of the Museum, 25 species of plants from the Campagna sprang up next year, and 4 became naturalised round Copenhagen.

Dewey states that *Verbascum phlomoides* and probably also *Bromus tectorum* and *B. sterilis* were introduced into Kentucky in the packing of crockery ware.

Stellaria media is believed to have been introduced into the Macquarie Islands in packing of machinery (Cheesman).

R. Brown (in "How Plants Were Distributed Over the Earth") says that *Asclepias curassavica* was introduced from Tahiti to New Caledonia as packing in a bolster.

A curious story is told by Mr. Mactaggart in the "Commercial Bent Grasses of Canada" (by M. O. Malte, *Ann. Report Nat. Mus. Canada*, 1928) of the introduction of *Agrostis tenuis*, a North American grass, into New

Zealand. He says (in 1927) about 70 years ago some Nova Scotian Highlandmen emigrated from Prince Edward and Cape Breton Islands, and sailed first to the Cape of Good Hope, then to Australia, and finally settled in New Zealand. Before starting, they filled their mattresses with hay, including the *Agrostis*, and travelled with them to New Zealand. They took the mattresses to their settlements in Auckland, and eventually discarded them. The seeds in the mattresses thus thrown away germinated, and *Agrostis tenuis* grew, and became an abundant species.

G. Lawson (in *Proc. and Trans. Nova Scotia Inst. Sc.*, iv, 167), in writing of the occurrence of the Heather *Calluna vulgaris* in Nova Scotia, at Cape Breton, states that there is a tradition that early emigrants from the western Highlands brought heather-beds with them from Scotland, and eventually threw them away, and the seeds in them grew. The plant is rare and curiously local in North America.

Drug and Dye Plants.

Some plants popular as drugs have been introduced into other lands, and have escaped from gardens, or in some cases owe their wide distribution to the seeds being carried about by man and casually dropped, or by being swept out of druggists' shops in waste.

Datura Metel is said by R. Brown to have been introduced into Europe by the gipsies. It has only established itself, however, in a few places in the Mediterranean region. *D. stramonium*, of North America, so commonly found on rubbish heaps in England, probably owes part of its spread to the sweeping out of druggists' shops, as also does the Henbane (*Hyoscyamus niger*).

I have already called attention to the dispersal in this way of *Scoparia dulcis*, and refer to that of *Cissampelos Pareira* further on. Besides these may be cited: *Xanthium strumarium* and *Carthamus tinctorius* in the East Indies, and *Ricinus communis*, *Cassia alata* (a well-known remedy for skin diseases in the tropics), *Croton Tiglium*, *Jatropha curcas*, the purging nut, *Eryngium foetidum* (a favourite Chinese drug) and *Asclepias curassavica*, a native of South America, now widely diffused all over the warm countries, and many other plants owe much of their distribution to their value—real or imaginary—as drugs. Travelling natives, whether professional doctors or not, often carry with them dried bundles of medicinal herbs, of which the seeds fall out, during their wanderings, by roadsides, and at their camps, and many are soon established there, and may spread. Occasionally drugs, and more commonly dye plants, were cultivated, and, the cultivation being later abandoned, the plants persist, and appear to form a part of the indigenous flora. Thus we have the Opium Poppy (*Papaver somniferum*) still persisting in the cornfields of Cobham and Darenth in Kent, as well as elsewhere, where, no doubt, it was formerly cultivated. It appears to have been introduced to England in Neolithic times, no doubt as a drug. *Acorus calamus*, introduced as a drug from temperate Asia, has spread over large parts of the world (*see* p. 656).

Dyes were naturally cultivated on a large scale, and of some of these the plants remain long after their cultivation has disappeared. In England we have still persisting the Woad (*Isatis tinctoria*), a plant of Eastern Europe, Dyer's Weed (*Reseda luteola*), in many parts of the country. *Morinda tinctoria* has long been carried about by Malays for the orange dye of its roots, and *Marsdenia tinctoria*, a substitute for indigo, was scattered about the Malay Peninsula. Most of these plants, introduced long ago by natives or Europeans, have spread of themselves far from their original localities.

SOME INTERESTING CASES OF DISPERSAL BY HUMAN AGENCY.

I gave an illustration (in the *Annals of Botany*, xxxvii, p. 13) of the difference between the rapidity and wideness in the distribution of species in more or less the same environment and circumstances, in the cases of *Galinsoga parviflora* and *Matricaria discoidea*, which I will repeat here. Both plants are of American origin, and belong to the order *Compositae*. They are weedy annual herbs.

Galinsoga parviflora occurred in Spain as early as 1794, and has since appeared in Holland, Germany (Berlin, 1812), Italy and Austria, more or less sporadically, and apparently as an escape from botanic gardens. It was probably introduced accidentally with other plants, but in the 18th century a good many very poor weeds were introduced from foreign countries and cultivated as rarities or curiosities. In England its first record is at Twickenham, where it was collected by Rudge before 1809. It is now abundant in vegetable fields round Kew, being first reported there in 1861. It has appeared at Guildford and in Hertfordshire, and in 1912 at the Tweedside, with other aliens brought in wool. It has not spread very far from the Kew locality, and appears not to have crossed the river. Sowerby reports it as having been introduced as an ornamental annual in 1796, and I have seen a specimen (probably cultivated) from Chelsea in 1802.

S. F. Blake writes to me that Cavanilles saw it growing in the Royal Gardens, Paris, in 1785, from seed sent by Dombey from Peru, and that he later found it cultivated in Spain. He says also: " It is a curious fact that in " America *G. parviflora* and *G. ciliata* occur almost entirely in the vicinity of " cities—at least, in the eastern part of the United States. One or both of them " are common in Washington, D. C., Cambridge, Mass., and Burlington, " Vermont, but they are apparently of very rare occurrence in country towns. " This appears to agree with occurrence of this plant in England."

In other parts of the world the earliest dates I have of the plant are Peru (whence it originally came) 1785, North America 1893, India 1845, Java 1899, New Zealand 1894, Africa 1912, Philippines 1928 (Mrs. Clemens in a letter). *Galinsoga* possesses fruits with broad scales, forming a pappus, by which it can fly a short distance, and thus appears to have a superior means of dispersal to those of *Matricaria*, which possesses no scales or plumes on the achenes.

Now, *Matricaria discoidea* (of which a full account is given under Seeds and Fruits Adhesive in Mud to Human Beings, etc., p. 534) reached England in 1869, and has now spread all over England and Scotland, and is quite a common plant in all counties, and although it reached England 60 years before the *Matricaria*, the *Galinsoga* has not made a quarter of the spread of the latter.

A. J. Ewart, in treating of the alien flora of Victoria, Australia (*Proc. Roy. Vict.*, xli., I, p. 59) gives several instances of the different rapidities with which introduced weeds have spread in Australia. He mentions *Oenothera biennis*, introduced in 1887, which now covers less ground than *Digitalis purpurea*, introduced in 1917. This is, no doubt, due to the sandy soil requirements of the former, which, though long ago introduced into England, has established itself only on sand-hills and sandy spots.

Myagrum perfoliatum, introduced in 1916, beat *Marrubium vulgare*, introduced in 1870. *Romulea Bulbocodium*, established in 1860, has hardly beaten *Hypericum perforatum*, introduced in 1880, and *Inula graveolens*, in 1893, overtook and beat *Gilia squarrosa*, which arrived some years earlier.

The differences in the spread of these plants is, perhaps, due more to the adaptability of the species to the local environment than to the dissemination factor, though the latter has clearly had some part in the competition.

A curious history attaches itself to *Glycosmis americana* Grisebach (*Rutaceae*), a small shrub with very inconspicuous white flowers and pinkish-white drupes, of no use or ornament, which now ranges wild in St. Vincent, the Bahamas, Cuba, and French Guiana, and appears to be spreading along the sandy coasts towards Brazil. It seems a most unlikely plant to have been introduced by man.

The genus *Glycosmis* is peculiar to the Old World, and is confined to India, Malaya, and China, except for the American plant. The key to the puzzle of a species occurring in abundance and apparently wild in western South America, was given by a note on a specimen in Kew Herbarium, which states that, according to Dr. Broughton, it was introduced from England by Hinton East in 1788, to Jamaica, under the name of the "Mandarin orange," and it is nothing more than *Glycosmis citrifolia*, a very common shrub in Hongkong. The species, very abundant in Malaya as well, is variable, and the *Glycosmis americana* is exactly the form which is common in China. Mr. East probably obtained either the seeds (which, however, do not at all resemble those of any orange) or young plants from some mendacious Chinaman as those of the "Mandarin orange," and carefully conveyed or sent it to Jamaica, whence the birds distributed the seeds to other islands and the continent of South America.

Cissampelos Pareira.—I have mentioned in my paper on the Distribution of Plants another case of puzzling distribution, and suggested a reason for it. The plant is *Cissampelos Pareira* (*Menispermaceae*), a slender climber with inconspicuous greenish flowers and small red drupes. It is found abundantly in hedges and waste ground over most of the tropics, except West Africa and Polynesia and all oceanic islands, but is common in India, East Africa, and the Philippine Islands, scarce in the Malay Peninsula and absent from Java. Its original home is probably South America.

The plant was at one time believed to be the source of the true *Pareira brava*, a drug highly valued by the Portuguese, but which was derived from *Chondrodendron tomentosum*, and as it appears in the Old World in countries where the Jesuit missionaries had establishments in the 17th century, it seems very probable that it was introduced by them to their settlements at Goa, Manila, and Malacca by mistake for the true *Pareira brava*, at the time that they were introducing many useful plants from the New World. Its spread since in Asia and Africa is due to the red drupes being eaten by birds, and the seeds so dispersed.

Tridax procumbens (*Compositae*).—This South American plant is now widely distributed in the tropics. It is a low herb with yellow flowers and plumed achenes. It appears to have been introduced as an ornamental plant originally to the Old World, and has established itself, not only in waste ground, but on sandy seashores, so that it often looks as if it was a native. It is certainly not cultivated at the present day.

It was introduced into India before 1830, and spread to the Malay Peninsula, Java, Papua, Queensland, Fiji, Nigeria, South Africa, Mauritius (where a note in Herb. Kew, dated 1864, states that it escaped from gardens 20 to 25 years before), Bourbon, Rodriguez, and other islands. It is abundant in America, from Florida and the West Indies, Mexico, and Colombia, where it is said to be wild in woods. Since its introduction, probably (though not showy) as an ornamental plant, it has spread by its plumed achenes.

Lantana mixta is a shrub now widely distributed all over the tropics. It seems to be a native of tropical South America, and was introduced into Europe in about 1737. After being cultivated as an ornamental shrub in Europe, it was sent to various botanic gardens, and from thence was widely distributed by birds, even to islands like Krakatau after the eruption; it, however, never reached the more distant ones, like Christmas Island.

Peperomia pellucida (*P. exigua* Miq.) (*Piperaceae*).—This is a small-branched succulent annual herb, 2 to 8 inches tall, with very slender spikes of minute fruits. A native of South America, where it is abundant in shady damp spots, it has been apparently accidentally carried to the Old World in introduced plants, and is usually to be found associated with botanic gardens, whence it has spread further. It is now found in Hongkong, Calcutta, Assam, Saigon, Singapore (common in the gardens and in other cultivated ground), Java, Amboina, Christmas Island, West Africa, Zanzibar and the West Indies.

It is not clear how it got from South America to the Old World, but doubtless in some pot plant brought across. It undoubtedly reached Christmas Island from the Singapore Botanic Gardens in that way, when Mr. Ross settled there and brought cultural plants from Singapore and Java. It appears to have been used as a pot-herb in Africa, and as a cure for the sting of venomous insects in the West Indies, but not elsewhere.

Portulaca oleracea, Purslane.—The very wide distribution of this plant is undoubtedly mainly due to human agency. Purslane was very early known as a vegetable in Europe, being mentioned by Pliny, and for a great many centuries was highly valued as a drug and pot-herb. It is probably a native of Northern Africa, and from its succulent habit was doubtless a desert or desert-border plant. It appears to have been one of the vegetables, the seed of which was carried about by early explorers and planted with other European vegetables in all parts of the world. It is known to have been carried to New Zealand by Captain Cook in 1774, and occurs now in all islands sufficiently warm where man has been, as well as in nearly all continents suited for its growth. It has somehow become unpopular as a pot-herb, and, though very common in the Malay region, neither Chinese nor Malays cultivate or eat it.

The seeds are certainly dispersed by rain-wash, and possibly, as they have been found in the stomachs of birds, have been to some extent disseminated by them. It used to spread very readily in the coffee estates of the Malay Peninsula, in spite of being constantly weeded out. It appeared in Christmas Island in cultivated ground, probably brought in accidentally in vegetable seeds or in soil attached to plants, but I only met with it in 1904.

Hemsley suggests that it is sea-dispersed, but I have seen no evidence of this. He says it is common in maritime districts, including the most remote islands and islets, being apparently one of the first plants to establish itself on coral islands, and adds that it seems more probable that its seeds or even branches are conveyed from shore to shore by the sea. (Challenger Expedition, vol. i). He records it from Bird Island, Seychelles, one of 6 plants found there, the remainder being sea-borne plants, on Maldon and Caroline Islands (to these it does seem to have been brought by sea); also on Diego Garcia, Chagos Archipelago, Fanning Island, Aru and Timor Laut. But there seem to be other human agency-dispersed plants on all these isles. Osbeck found it in Ascension in 1750, and in 1776 Sparrmann found it abundant in St. Helena and Ascension. Both of these islands had, however, been often visited nearly 200 years previously, and extensive settlements and agriculture centres had been established in St. Helena long before this. It is recorded in Massachusetts in 1672, no doubt brought intentionally as a pot-herb.

That this plant's seeds may have been dispersed by sea occasionally seems likely, as it is difficult to account for its appearance on some of the islands mentioned by Hemsley, otherwise its absence from Christmas Island, till brought with cultivated plants, from Cocos-Keeling Island, Krakatau and other small islands, suggests that the occurrence is rare. Though Hemsley states that it is especially common in maritime districts, I have seldom seen it in such spots, but more commonly in cultivated land in the interior.

Drymaria cordata (*Caryophyllaceae*).—This is a slender straggling weed which grows chiefly in cultivated and waste ground, like a chickweed. The genus is well represented by a number of species in South America, including *D. cordata*, which has spread widely over the warmer parts of the world. In 1921 I found it abundant in the garden of the Rest-House at the top of the Semangkok Pass, between Selangor and Pahang, in the Malay Peninsula, and along the roadside leading down the descent of the Pass. I had frequently botanised at, and round, this spot previously, and had never seen it before. From what I can gather, it had been introduced in rose tree roots from Java, where it is common at high altitudes, usually in cultivated ground, and it has probably been thus introduced into the Old World from South America at an early date, very much in the same way that the common European chickweed has been conveyed about the world. It is now abundant in tropical Africa, Madagascar and the Comoro Isles, Seychelles (known to be introduced), China, India, Siam, Sumatra, Java, the Philippines and Papua, Hawaii (1895), South America and West Indies, and Galapagos (1867). The Papuan locality, high up at 6,000 feet, never previously visited by Europeans, seems a puzzling one, but the presence of this plant may be accounted for by the fact that the mountain folk cultivate sugar-cane, sweet potatoes, colocasia and ginger there, and the seeds may have been carried up from the lowlands in soil attached to these plants, obtained probably from Dutch cultivations.

Oxalis corniculata.—This little creeping plant is very widely spread all over the world, mainly by human agency. It is certainly a native of Southern Europe, and was described by Clusius as coming from that region in 1549. In most parts of the world it is only known from greenhouses and cultivated land, but it is probably also native in the north temperate zone of the Old World, being specially common in India, where there is a hairy form which also occurs in other warm parts of the Old World. The capsule is explosive, and contains a large number of small seeds, which probably get into pots or among the soil attached to plants, in which it is conveyed across the globe. It is met with in Europe to Asia Minor, Palestine, Morocco, Canaries, Madeira, Azores, China, Japan, India, the Malay Peninsula, Java, Sumatra, Borneo, Philippines, Australia (1802), New Caledonia, Lord Howe's Island, New Zealand (1838), Kermadec, Oahu, Easter Island (1917), Cook Isle, Gambier Isle, Solomons, Sandwich Isles, Isle of Pines, Rapa, tropical Africa (rather sporadically), Socotra, South Africa, and North and South America. It is absent from islands not cultivated by man, so that it seems clear that its seeds are carried about accidentally. It seems remarkably abundant in the Polynesian Islands, where it appears to have been established before the advent of Europeans.

Oxalis stricta, first sent by Clayton from Virginia in the 18th century, is less widely distributed, but is not rare in parts of Europe, etc. It is certainly an American plant, and seems in other countries to be always a garden escape.

There are a large number of species of *Oxalis* in South Africa, and some of these have been cultivated for ornament, and are abundant, and appear quite wild in other parts of the world. One of these is *O. corymbosa*, with fine pink flowers. This produces underground bulbs, and is diffused by means of these spreading, sometimes extensively. It seems rarely to fruit outside its own country, South America. It is now well established in Madeira, Canaries, Azores, India, Ceylon (Moon 1817), Penang, China, Japan, Jamaica, where it is abundant in the forests.

Henslow (*Journ. Roy. Hort. Soc.*, xxxv, 342) gives a full account of the yellow-flowered *O. cernua* of South Africa, which has become established in the Mediterranean region and the Canaries, Madeira, and the Bermudas. It first appeared in Malta in the Botanic Gardens at Valetta in 1806, then in Lybia 1824 and in Gibraltar 1826, and in Egypt apparently introduced to

Cairo in orange trees from Malta about the same time. It reached Sardinia about 1837, and Algeria before 1847. Parlatore, in 1848, describes it as growing near Naples, Sicily, Corsica, and near Smyrna. It does not appear to have reached the Canaries before 1840, for it is not mentioned by Webb and Berthollot in their "Histoire Naturelle des Iles Canaries." Henslow thinks that the plants found in the Canaries and Madeira came direct from the Cape itself, and not from Malta. He found it at Cannes in 1892, and says a single plant was introduced into M. Constant's garden in some Palms. These exotic species of *Oxalis*, *O. corymbosa*, and *O. cernua* are, in their new homes, entirely propagated by bulbils borne on thread-like lateral roots (more strictly, probably rhizomes), and *O. cernua* often produces runners above ground also, which bear bulbils. These two plants may be contrasted with *O. corniculata*, which propagates by seed only, and is much more widely distributed than the bulbiliferous species, though these are very abundant in the localities in which they have been introduced. Indeed, I have seen *O. corymbosa* so well and widely distributed in Jamaica that the plants were quite abundant in the woods some way from cultivation, and had all the appearance of being as native as any plant in the surrounding forest. Both groups of *Oxalis* owe their extensive range to human agency, but the seeding *O. corniculata* goes further and to more distant localities than those propagated only by bulbils.

It is quite possible that some of the seeding *Oxalis* are distributed by birds, as otherwise I cannot account for the two endemic species, *O. noronhae*, and *O. sylvicola*, occurring in Fernando de Noronha.

Cardamine hirsuta (*Cruciferae*).—This little Rock-cress, so abundant in England and all over Europe, seems to have originated in the Antarctic regions and travelled north. *C. tetraphylla*, of Australia and New Zealand, certainly indigenous, seems to be a large form of it. The more common forms occur in Europe, Asia, India, Siam, China, Java, more scantily in tropical Africa, Mauritius, and North America; in most, if not all, these localities it appears to have been introduced in pots and soil. I once found it in Singapore in a rubbish heap, where pots of plants from Europe had been emptied, but it rarely exists in hot climates.

Stellaria media, the Chickweed (*Caryophyllaceae*) is a well-known English weed, which has been carried all over the world in seeds or pot plants. It is known to have occurred in Britain and on the Continent in pre-Glacial days, and while it has largely been spread over the north temperate region by cattle, yaks, and other herbivorous mammals eating it and passing the seeds, and probably also carrying them in mud on their feet, it has been more widely spread by transportation of its seeds in soil and vegetable seeds. Hooker records finding the chickweed, with *Poa annua*, on a French sailor's grave in Auckland Isles when he first visited it. Probably a pot of some flower was planted on the grave, the soil of which contained seeds of these two common European weeds.

It was found in Australia in 1802, and Cunningham found it far from the Settlements in New Zealand in 1834. It has also been found in the Falkland Isles, Amsterdam Isle, St. Paul's, St. Helena, in Abyssinia, and scattered about in other parts of tropical Africa, Mauritius and Madagascar, Bourbon, and South Africa, and in South America. It twice appeared in the hill-gardens of Perak, Malay Peninsula, where many rose bushes, violets, and other European plants had been introduced. It appeared in the Macquarie Island (1894) near the factories, probably brought in packing for machinery, and also near the sealers' huts, brought, perhaps, in mud on their boots.

Cnicus lanceolatus, the Spear Thistle, has largely been spread by human agency, accidentally; but Ball (in "Notes of a Naturalist," p. 165) states that an Englishman imported a sack of the seed, which he spread broadcast in

the neighbourhood of Concepcion, Chile, thinking it would be useful as a fodder. It is now abundant in Chile. It appears also to have been brought in grain.

Crepis japonica.—This little annual Composite, with very small plumed achenes, the pappus of which falls off very readily, is apparently a native of India, but now widely distributed to China and Japan, the Malay Peninsula,* Java, Sumatra, Borneo, Amboina (found by Rumph about 1741), Papua, Australia (1802), Mauritius (1835)*, Natal*, Fiji, Hawaii, San Christobal, Jamaica* and Guiana*. (In the places marked * it was almost certainly introduced in pot plants. It serves no use, and is not ornamental. How it got to the other localities is obscure, possibly in baggage.)

Erechthites valerianaefolia, a South American grass somewhat resembling a sow-thistle, with pink flowers, is now distributed in waste ground in tropical Asia. According to Hasskarl, it was brought to Java in coffee seed from Brazil, in 1845, by General Rochussen. It is now abundant in the Malay Peninsula, Java, Sumatra, Borneo and Amboina, and has occurred rarely in South India and Ceylon, and reached Krakatau by 1919. The plumed achenes are spread by the wind, but the plant seems to be moving but slowly.

Polycarpon tetraphyllum (*Caryophyllaceae*).—This little prostrate herb is now spread all over the world, and the causes of its very wide distribution are not at all clear. The minute seeds are not buoyant. The plant in a wild state occurs largely on sandy spots, chiefly near the sea. In Guernsey, where it is abundant, I found it only on dry places on cliffs, well above the sea, but it is also found on roadsides and in waste ground. In Egypt, and the Azores and Canaries and most of Europe, it is found on walls or roadsides or in cultivated ground. In Tasmania, Gunn writes (on a label in Kew Herbarium), "probably imported, as I only find it in places where it is likely "to be scattered with imported seeds." In its native state it seems to occur on rocks or sandy shores by the sea, and is probably truly wild in the North African and perhaps Indian regions. It occurs in Southern Europe, Egypt, Africa to the Cape, India, Burma, Ceylon, Cochin China, Siam, Yunnan, China (these are the leafy forms known as *P. Loeflingi* and seem chiefly associated with river sand-banks), North and South America and the following islands, Azores, Madeira, Cape Verde, Ascension (1843), St. Helena (1865), Tristan d'Acunha (1852), Australia (1834), New Zealand, Madagascar. In the islands and Australasia there can be little doubt that the plant has been introduced by man, either in weed-seeds or in ballast, and by one or other of these ways it seems probable that it has reached America, and perhaps other districts. However, it appears also to be dispersed by the adhesion of its seeds to the feet of birds.

Lochnera rosea (*Apocynaceae*).—This shrubby erect periwinkle was first introduced into Europe from Madagascar to Paris in 1768, for its ornamental flowers, and from there has been distributed all over the tropics, where in very many localities it is so abundant on the sea shores as to appear native. It appears also to be indigenous to India. It is now a characteristic element of the floras of China, Malaya, Papua, many Polynesian Islands, Samoa, Tonga, Sandwich Islands, Easter Island (" half savage," as a collector in Kew Herbarium describes it), tropical Africa, the West Indies, and South America. The seeds are not plumed, as in most of the order, but oblong-linear and rather corky. It is possible that they may be dispersed along the sandy shores by the waves, or, more probably, blown along by wind, but it is absent from remote islands. Indeed, it clearly owes most of its distribution primarily as an ornamental plant.

Acorus calamus (*Aroideae*).—This water plant appears to have originated in Central Asia and Northern China, the only other species of the genus,

A. gramineus, being found in China and Japan, with outlying localities in Tonkin and Assam. *A. calamus* was brought to Europe in early days, it being formerly highly valued as a drug. It seems first to have been known to Dioscorides and Pliny A.D. 23 to 79. Celsus (25 B.C. to A.D. 50) mentions *Calamus Alexandrinus*, probably brought from India to the Red Sea. It is said to have been introduced into Western Europe in the 13th century. It does not fruit in Europe, nor in most countries, but has become common in England from its rhizomes drifting in the rivers. It at present occurs in most parts of Europe, Asia, temperate China, Japan, North India, the Malay Peninsula and North America. It is commonly planted in gardens by Malays, Chinese, and other Oriental tribes, who still use it as a drug.

Poa annua.—This very common little grass is probably a native of the whole north temperate zone, certainly of Europe and temperate Asia. It is found in Arctic America, and may be indigenous to temperate North America. The small grains are spread about by wind, the outer glumes acting as wings, and to some extent by rain-wash, but it owes its very wide distribution mainly to human agency.

Hooker records finding it with the Chickweed (*Stellaria media*) on the grave of a French sailor in Auckland Isles, doubtless due to its seeds being brought in the soil attached to some plant planted on the sailor's grave. In the Malay Peninsula it has twice appeared in some quantity as a weed in the gardens on the Perak hills, brought there from Europe in soil attached to pot plants. In Sumatra it is found at Berastagi and other localities where vegetables, potatoes, and European pot plants have been planted. Once planted, the wind and rain disperse the grains as far as the plant can grow, its spread being checked by heat, shade, or unsuitable soil. It was probably disseminated very early.

The grass seems very abundant in India, and, as has been mentioned, occurs in the Malay Peninsula and in Sumatra, also at Luzon in the Philippines, Tasmania (1837), Macquarie Islands (1894), Kerguelen (1874), Tristan d'Acunha (1852), Gough Island (probably brought from the last-mentioned island) in 1914, St. Helena (1808), St. Paul (1853), New Zealand (1843), Arabia, South Africa, Bourbon, Mauritius, Sandwich Islands (1865), North America, along the Andes at Ecuador to Monte Video and the Falkland Isles, and in Juan Fernandez (1875) besides, of course, all over Europe.

In most of the Atlantic islands it was perhaps brought accidentally in vegetable seeds, but in some places undoubtedly with grass seed for pastures, as has been the case with *P. pratensis* in Kerguelen, Antipodes Island and Auckland. At Macquarie Island the plant was found by the sealers' huts with *Stellaria media* and *Cerastium triviale*, and in many of the islands *Sonchus oleraceus* accompanied these plants. These 4 weeds are apparently the most regular travellers with man in the colder parts of the world.

Eleusine indica (*Gramineae*).—This grass is very widely spread all over the world. It is a rather stiff grass, with short stout peduncles bearing a number of short or long spikes of densely-set spikelets at the top. The spikelets are unawned, the outer glume roughly scabrid on the keel, but it does not appear to be in any way adhesive to fur or clothing. It is now one of the most common grasses over all warm countries, usually growing in dry spots, roads and paths, and waste ground. It is probably of Indian origin. A cultivated form of it, *E. coracana*, is used as a millet, and has been carried about to various parts of the world, but is seldom used outside India. I have no knowledge of any spot where *E. indica* occurs unassociated by man, nor of any island where it was impossible for it to have been brought by man. It is given by Guppy as one of the original weeds found by Capt. Cook's botanists, Banks, Solander, the Forsters, etc., in 1768, in Tahiti, practically before any other European had ever landed there. There is no evidence that its seeds can be sea-dispersed,

and it is not a seashore plant, nor is there any proof of its being carried by birds. It is certainly dispersed by rain-wash and by cattle, horses, etc., which feed on it. In Africa it is very common, and used for cattle fodder, and the seeds are thus dispersed, and it has sometimes been conveyed in garden soil, but none of these methods seem to be enough to account for its early and wide distribution. It has been found in the following localities, of which the earliest dates of the more important ones are given, so far as I am able to find them :—Spain, Egypt, Canaries, Cape Verde Isles, Madeira, Azores (1856), China, Japan, India, Malaya, Tahiti (1768–80), Sandwich Isles (1825), Australia (1845), Africa, St. Helena (1868), Christmas Island (1890, before the introduction of any domestic animals), Cocos-Keeling Island (1911), Krakatau (by 1911) America, Galapagos (1905).

In the Atlantic isles and Europe it is usually a street plant, as it grows very readily in gravel paths, cracks in masonry, and such spots. In Christmas Island it grew only in cultivated soil, and was probably brought in earth with other plants; Mr. Clunies Ross had settled there in 1888, but no cattle were brought till some years later. In Krakatau it was found in 1919, but not in the earlier collections; there had been a short temporary Settlement in the island previously, and, as I have already suggested, it might have been brought accidentally by one of the earlier expeditions.

Cryptogams, except many parasitic plant fungi, seldom owe their dispersal to man. Among ferns, *Cheilanthes farinosa*, *Adiantum capillus-veneris*, and some other species have escaped from cultivation, and the accidental introduction of *Pteris aquilina* by spores in baggage to the Tahan plateau has already been mentioned. A few woody fungi, e.g., *Schizophyllum commune*, *Guepinia spathulata*, *Polystictus sanguineus*, have been carried about in timber, but I know of no other Cryptogams transported by man except some marine *Algae*.

Marine *Algae* may be dispersed and transported by man, by being attached to ships, and being so carried from one place to another throughout the world. At present I can find very few observations on this subject recorded. C. H. Ostenfeld, writing on the immigration of *Biddulphia sinensis* and its occurrence in the North Sea, gives an account of the sudden appearance in 1903 of this diatom from the Indian and Pacific Oceans into the North Atlantic. It was found abundantly in an area of the North Sea, extending westwards to the mouth of the Elbe, and eastwards to the Skagerak Kattegat. By its sudden appearance within a restricted area of the North Sea it is improbable that it was carried there by sea-currents, and he concludes it had been brought from afar by ship, probably from the Indian Ocean, either attached to the outside, or in water in the hold, or in a disused bucket, in one of the steamers trading to Hamburg, especially as its first recorded occurrence is off that port. It has now spread, since 1903, along the Belgium and Dutch coasts, and along the west coast of Norway, but has not yet (1908) reached English waters.

Some *Algae*, especially diatoms, have been introduced into various parts of the world by man on imported water-lily roots and other aquatics.

Conclusion.

Considering the immense number and variety of species of plants introduced into new countries, especially during the last century and a half or two centuries, into botanical and private gardens, it seems remarkable that such a small percentage have ever established themselves as real inhabitants of the surrounding country. Many plants easily grown, with practically little or no attention, have entirely failed to establish themselves outside the garden. In some cases, undoubtedly, competition has restricted their diffusion, but there

are other limiting agencies which seem quite obscure. Except cornfield weeds, few introduced species have really established themselves sufficiently to form part of the British flora. *Pyrus aucuparia*, introduced in Neolithic times, *Acer pseudo-platanus*, introduced much later, and some roadside weeds, are almost all. The alteration of the soil, by man's agriculture, is, of course, responsible for the appearance of the cornfield weeds, and the formation of roads has also formed localities suitable for certain plants. Complete change of environment, alteration of soils, sunlight, rainfall, and temperature, and (probably equally important), underground movements of water effected by man in clearing forest and cultivation of the soil, have undoubtedly changed the flora of any locality to an enormous extent, but in most cases an equilibrium is formed which prevents further change, till another alteration takes place, and during this state of equilibrium few, if any, new species can establish themselves.

CHAPTER X

MECHANICAL DISPERSAL

Plants aided in Dispersal by Elongate Stems or Rhizomes—Dispersal by Bulbils—Explosive Fruits—Fungus Spores and Sporanges Discharged by Explosion—Propulsion of Bulbils.

PLANTS AIDED IN DISPERSAL BY ELONGATE STEMS OR RHIZOMES.

Plants which possess long-trailing or creeping stems, at the ends of which fruits may be borne, possess a distinct advantage over tufted plants, and may spread considerably faster. Creeping grasses overlying tufted ones can kill the latter out, and by covering the soil in a mat can, in hot weather, cause the retention of moisture below their leaf-mat. The success of *Trifolium repens* in exterminating tufted plants is due largely to this. Its action in the destruction of *Phormium tenax* has been already mentioned. The Lalang grass (*Imperata cylindrica*), with its subterranean rhizomes, can hold its own against other competitors, chiefly on account of the fact that, while a casual fire will almost completely destroy all other vegetation on the ground, the rhizomes are protected, and after a fire are no worse for the accident. This form of evolution is, however, rather an aid in the competitive struggle for existence than assistance in the actual plant-dispersal. It is, however, of importance in spreading the plant locally for some yards distance, as every gardener knows in the case of such plants as *Convolvulus arvensis*, *Calystegia sepium*, *Rumex acetosella* and *Aegopodium podagraria*, which spread rapidly and continuously to a considerable distance underground by their rhizomes, far more rapidly than by their fruits. Fragments of these creeping stems may also be accidentally carried about by human action, rivers, etc., and so be dispersed. The spread of a plant by underground rhizome or creeping stem is comparatively slow, it is true, but it must be taken into account in the dispersal of species; a plant which can creep only 1 yard a year will have spread in all directions upwards of 1 mile in 1,500 years by this method alone, but many plants grow much faster than this. *Ipomoea biloba* and *Canavalia rosea*, on sand-banks, run to very many yards; *Ischoemum muticum* will throw out creeping stems reaching to a distance of 12 or 14 feet; *Nepeta glechoma*, the Ground Ivy, runs to as much as 12 or even 20 feet along the ground. The Elm, as I have found by measurement, can reproduce itself by suckers from underground roots at a distance of 50 yards from the parent tree, and *Robinia pseudacacia* creeps in this manner for 30 yards. The Elm (*Ulmus campestris*), which appears, in England, never to reproduce itself by seed, has in this way spread all over the country. The spread of aquatics by rhizome, such as *Acorus calamus*, all over Europe, has been already described under River Dispersal (p. 182), as has the wide spread of long-stemmed aquatics, *Elodea canadensis*, *Potamogetons*, etc., by water and birds (pp. 177 and 536). I may, however, mention here *Utricularia fluviatilis*, a species with stems many yards long, which I found in abundance in the Johor River at Kota Tinggi, in the Malay Peninsula; the only flowers I could find were in one shallow backwater. This plant seemed

to have spread for miles almost exclusively by its vegetative organs. Another way by which plants spread vegetatively is by layering of the branches. The Blackberry (*Rubus fruticosus*) is said to have covered large areas in New Zealand by the rooting of its branches when they touch the ground.

The spread of the *Cacti* in the American deserts and prairies, by means of their joints, seems largely to have replaced their dissemination by seed. Toumey says (in "Vegetal Dissemination of *Opuntias*") that in the *Platopuntias*, which are prostrate or semi-prostrate, the branches creeping on the ground root at each joint. Of *Opuntia phaeacantha*, near Tucson, he found 20 plants which had radiated from a common centre for as much as 20 rods from the original centre. Of *Opuntia Bigelovii*, which he says is mainly dispersed by attachment of the joints to cattle, he writes :—" This plant has almost lost its powers of " seed-dissemination ; out of 50 plants, 48 were sterile (seedless), and 2 had " but 1 seed apiece." The adaptations for vegetal dispersal are inversely proportionate to their seed production.

Another advantage in dissemination by creeping rhizomes is the carrying of the seeds to a long distance from the original plant. Thus, if a Sea-Convolvulus (*Ipomoea biloba*) has stems 20 feet long, the seeds borne on the terminal portion start to grow 20 feet away from the parent, and, continuing to spread another 20 feet, may make a very rapid growth over a sand-bank. Furthermore, the further the stem grows, the more flowers and fruit can be produced. It is probable that the far greater abundance and wider distribution of *I. biloba* than that of *I. carnosa*, which has the same method of seed-dispersal, is due to the long creeping stems of the former ; and here may be mentioned the spread of *Linaria cymbalaria* by its branches, bearing fruits, creeping along the walls and depositing seeds farther along in crevices.

DISPERSAL BY BULBILS.

A number of plants of various orders are reproduced mainly or altogether by bulbils produced in the axils, or on the inflorescence, where they replace the flowers, and these plants often owe much of their dissemination to these bulbils, which are dispersed in various ways. In some cases the bulbils merely fall off from a tall inflorescence (in *Fourcroya*), some when small (*Allium vineale*) only by rain-wash after the fall of the inflorescence, occasionally they are drifted by river, as in *Ranunculus ficaria*, but many of them are too heavy to be so dispersed. In the case of *Polygonum viviparum* the bulbils are often swallowed by birds, and pass through the intestines unharmed. The bulbils produced by the Aroid *Remusatia* have hooked leaves, which are adhesive to birds, and those of the *Poa alpina* are dispersed by wind.

Bulbils in some plants entirely replace the flowers. The form of *Allium vineale*, which bears bulbils exclusively, is much more common than the flowering form. Where, by change of environment or climate, the production of seed capsules is prevented, some plants maintain their existence only by bulbils or detached buds.

In the Malay Peninsula, in many spots in the dense forest, one meets with plants of a *Cycas* quite indistinguishable from *C. Rumphii* of the seashores, but which never produce male or female inflorescence. In some places I have found the trees growing at the foot of the limestone rocks, which, though now over 30 miles from the sea, are traditionally said to have been at the sea-edge within human times. These forest *Cycads* produce bulbils or large axillary buds on the stem, which become detached and roll down the hill-slopes, or are washed down by the rush of rain, and, when they come to rest, take root and eventually develop into trees. It is easy to understand that if these *Cycads*,

growing on the seashore, become involved in the advancing forest, growing over the new land formed by the denudation of the mountains silting up the shallow seas, it would be impossible for them to be wind-fertilised, as the dense forest would prevent the pollen from reaching the female plant. Unless they produced bulbils, and so reproduced themselves, these *Cycads* would die out.

In Christmas Island is a species of *Cycad* which was very abundant there in 1897, when Andrews visited the island. It seems since then to have become scarce, for in 1904 I saw only 4 plants, all at considerable distances apart. No inflorescence or fruits of the plant have been seen, nor could I find on the plants I examined any sign of their ever having flowered. The species has been referred to as *Cycas circinalis* var. *javana*, but is more probably a form of *C. Rumphii*; however, without flowers or fruit, it is not possible to identify it. It produced on the stem axillary buds, 2 of which I took to Singapore, where they readily grew. There can be no doubt that the ancestors of this plant were derived from sea-borne seed, as the seeds of *Cycas* often occur in sea-drift; but the plant has long given up fruiting, and reproduction by bulbils has taken its place, the bulbils, when detached, merely rolling about over the rocks till they find a place to root in.

Here I may call attention to the *Pandani*, which are unisexual plants common in the Malay forests. Of 30 species, the male flowers of only 8 are known, and of these, though often common plants, of several I have only once seen a male plant, and never fertile fruits. Of one species long cultivated by natives for its scented leaves, neither male nor female inflorescence has ever been seen, it being propagated by cuttings.

It seems certain that none of these Pandans have reproduced themselves by seed for many years, yet they are scattered all over the forests, more or less sporadically. I believe that they are merely disseminated by detached fragments being drifted about the forests by wind and rain.

Bryophyllum calycinum (*Crassulaceae*) is a succulent herb, a native of Africa, which has now spread all over the world, having been introduced into many parts on account of its curious habit of producing bulbils on the leaves, whether attached to the plant or cut off and hung up in a damp spot. From these bulbils the plant is easily propagated. It seems, in most parts of the world, to be propagated exclusively by them, seldom fruiting. It is very curious to see the plant in the hedgerows of Jamaica, after rain, with all the leaves fringed with bulbils. The bulbils are doubtless distributed by rain-wash after the decay of the leaf.

The lesser Celandine (*Ranunculus ficaria*) produces small tubercules or tuber-like shoots in the axils of the leaves, often in great abundance. They fall to the ground with the withering foliage in early summer, and are dispersed by heavy rains. When the rain is so heavy that the water flows away in rivulets, the loose tubers are washed off in abundance. A sudden downpour of rain in a region abundantly supplied with Lesser Celandine is sufficient to float away numbers of the tubers, and heap them up on the borders of irrigation channels when the rain disperses. In such cases the quantity of tubers which have floated together is so large that one can hardly gather them in one's hands (Kerner and Oliver, ii, 810).

The large green Aloes (*Furcraea*) of South America have long been introduced into the Old World, chiefly for cultivation for leaf-fibre, but they are also largely grown for fences in Southern India and elsewhere. They throw up a very lofty spreading panicle, but in the Old World the flowers are not yellowed by the formation of fruit, but by a large development of bulbils. When the panicle falls, the bulbils are thrown to the ground, where they continue to grow. They may be further dispersed by rain-wash. I saw *Agave americana* also producing bulbils in South India in a similar way. In these

cases evidently reproduction and dispersal by bulbils or detached shoots are more advantageous to the species than reproduction by seed, and are, perhaps, due to change in the environment of the plant.

EXPLOSIVE FRUITS.

Most herbaceous plants which have a number of seeds in a capsule (unless these are plumed, winged, or light enough to be carried away by the wind or by river), depend on the violent shaking of the raceme, spike, or panicle for their dispersal away from the mother-plant, as I have described under Jactitation (*see* p. 16); but a certain number of plants, chiefly herbs, have a mechanism by which, on maturity, the capsule explodes and throws the seeds to a considerable distance from the parent. As in the case of the other plants mentioned above, it is usual for this class of seeds to be further dispersed by rain-wash or river or by ants, for the actual distance to which they go is usually not very great, varying from 3 or 4 feet to about 40 feet (*Hevea*), or, in the exceptional case of *Arceuthobium*, as much as ¼ of a mile.

The seeds in an explosive fruit are usually few in number, from 3 or 4 up to about 20.

Plants with explosive capsules belong to a variety of orders, and though a few orders, such as *Acanthaceae* and *Balsaminaceae*, have in almost all cases explosive fruits, in some genera we find that only some of the species have such fruits, the others having capsules which merely dehisce and let the seeds fall on the ground. Thus while in *Viola canina* and some other species the seeds are thrown out explosively, in *V. odorata*, *V. hirta*, *V. tricolor*, etc., the capsules do not possess the mechanism of explosion. Again, the 3-celled capsule of the dwarf *Phlox Drummondi* explodes and throws its seeds about, while the fruit of the tall *P. paniculata* is 1-seeded (the other ovules being suppressed) and is almost drupaceous.

The mechanism for the violent explosions of seeds is very varied. In one series the explosion is due to the increase of pressure in the fruit during ripening either of the walls, or of the contents of the fruit, or of part of the stem below the fruit, with a resistance to dehiscence of some part of the fruit or stem, which is only overcome by a loss of water, or by a shock, when the dehiscence takes place suddenly and violently.

Thus in the capsule of an *Iris* or Lily the dehiscence commences at the top, and gradually continues downwards. In *Alstroemeria* the capsule remains closed till, owing to dryness, the pressure on the 3 valves becomes so great that, as soon as the resistance is overcome, the capsule instantly flies into 3 valves, the placentas spring up, and the seeds are thrown about in all directions; fruits of this series are found in the *Acanthaceae*, *Balsaminaceae*, and *Euphorbiaceae* and *Leguminosae*. In another series the capsule dehisces, but retains the seeds till desiccation of the valves takes place, which causes a pressure strong enough on the sides of the seeds to shoot them out, as in *Viola*, *Hamamelis*, etc.; or the inflorescence or perianth shrinks from the loss of water, till by pressure on the seed it ejects it, as in *Dorstenia*, *Arceuthobium*, and *Sloetia*; the seeds in these plants are usually smooth and rounded, often polished, but in many cases flat and discoid. They seem never to be roughened or papillose.

The distribution of some of the plants possessing explosive fruits is very extensive, as in *Impatiens* (*Balsaminaceae*), found in most of the Old World, with a few in America; *Acanthaceae*, all tropical and subtropical regions; *Euphorbia*, the whole world; the *Papilionaceae*, *Viola*, *Geranium*, *Montia*, all wherever the climate suits them; but some of the genera and groups are comparatively local, and they are usually absent from oceanic islands, unless supplied with other modifications for dispersal.

There is no doubt, however, that the scattering of seed by explosion is (at least locally) of very great value to the plant.

Among the *Cruciferae*, *Cardamine impatiens* (Pl. XXII, 11) and *C. hirsuta* have explosive pods in which the narrow linear valves, remaining quite soft, curl up suddenly on being touched, when ripe, much in the same way as do those of the Balsams, but in the reverse way, the valves curling up outwards instead of inwards. The seeds of these plants do not fly to any great distance, as the plants are only a few inches tall. Kerner gives the flight of the seeds of *C. impatiens* as about 2½ feet distant. I find those of *C. hirsuta* fly from 6 inches to 2½ feet. This is enough, however, to scatter the seeds away from the parent plant.

Like these low herbs are the explosive-podded *Corydalis* (*Fumariaceae*). Farrer (in the "Rainbow Bridge," p. 165), talking of *Corydalis curviflora*, of China, says: "Come too early, and the pods are hard and green; turn "away your head to sneeze, and, when you next look, the pod has burst open like "a popgun and shot out all its little glossy bullets."

Impatiens (*Balsaminaceae*).—These are herbs which usually inhabit shady woods or open rocky damp spots, and are not rare on stream banks. They are chiefly tropical and subtropical, a few occurring in temperate climates. The largest number are found in tropical Asia, 2 or 3 in Europe and 2 in North America, and about 20 in Africa. The capsules are fleshy, of 4 or 5 carpels, usually subcylindric, often dilated at the upper end, where the seeds are borne. The walls of the fruit consist of 3 layers of cells, the inner one being of large turgid cells. When ripe, spontaneously or if touched, the 5 linear carpels separate suddenly and roll up inwards, throwing the seeds out to some distance (Pl. XXII, fig. 6). The American *I. fulva* (*I. biflora*) is a riparian plant, and the seeds are thrown frequently by the explosion into the water of the stream on which it grows, and, as they are buoyant, are carried away and so further dispersed. The plant was formerly introduced to the Wey River, and is spreading down the Thames and other rivers (*see* Floating Seeds, p. 204).

In *I. parviflora* the seeds do not float, and the plant spreads much more slowly; but though the seeds only fly a few feet in exploding, the plant introduced into my garden spread about 40 feet in a year across the plots.

The taller plant, *Impatiens Roylei*, which is a native of the Himalayas, and has established itself as a garden escape at Looe, in Cornwall, and elsewhere, throws its seeds, on the explosion of the capsule, for a distance of 15 to 21 feet.

Oxalis.—These little herbs have a wide distribution all over the world, but those that are most widely dispersed owe much to the assistance of man. The seeds are dispersed by explosion in a manner different from that of other plants. In *O. corniculata*, a common creeping little weed, the pod is cylindric and elongate, and, if touched when ripe, suddenly splits open for its full length, and throws the seeds to some distance. In *O. acetosella*, the pod, green and fleshy like that of *O. corniculata*, is rounded, and dehisces by slits in the sides, and the seeds are shot out laterally. Frequently in both plants the dehiscence and seed-explosion are simultaneous, but sometimes the dehiscence precedes the flight of the seed. When ripe, the seeds are surrounded by an abundant mucilage, and, according to Chauvel and Bullerstaedt, the mucilaginous layer over the seed contracts and splits from the seed. The layer, drying, rolls up with rapidity as the mucilage contracts, and the seed is shot out much as the stone of a cherry is when the fruit is pressed by the finger and thumb. V. Royale (*Ann. Nat. Sci. Paris*, 1918, p. 25) gives a slightly different account of the dispersal of the seed in *O. acetosella*. He states that the tegument of the seed consists of an epidermis, parenchyma and a layer of thick-walled cells. Each seed is surrounded by a mass of mucilage, which fills up the spaces between each seed, and between the seeds and cell-wall.

In most cases the tegument of the seed remains attached to it after dehiscence, but in *O. acetosella* he has seen it two or three times left behind in the cell. He thinks the dehiscence of the tegument is not the cause of the explosion, but the mucilage, by swelling, carries the seed against the slit, the resistance of the cell-wall is overcome, and the seed shot out. The distances to which the seeds fly is about 2 or 3 feet, so far as I have seen in *O. corniculata*. E. Walker (in " Autosporadic Seeds of *O. stricta* ") gives the distance he measured as 3 feet (Pl. XXII, fig. 20).

The dehiscence of the Squirting Cucumber (*Ecballium Elaterium*) is quite unique in the vegetable kingdom. The plant is a prostrate herb inhabiting dry spots on the Mediterranean coasts, and also is found in the Azores, but probably reached there in ballast, as it has done in other parts of the world. The fruit is an oblong berry about 2 inches long and 1 inch through, borne on a stout peduncle, and usually lies on or near the ground. The apex of the peduncle projects into the base of the fruit like a stopper. When the fruit is ripe, the tissue surrounding this stopper breaks down, so that the connection between the fruit and the peduncle is loosened. The seeds are now surrounded by a quantity of a semi-liquid mucilage. In the wall of the fruit a layer of cells now undergoes great tension, endeavouring to stretch out. When the tissue at the base breaks, the fruit is suddenly detached from the pedicel, and the strained layer of tissue, in becoming stretched out, forces out the seeds through the hole in the base with great violence, with abundance of mucilage. The explosion throws the seed to a considerable distance, sometimes nearly vertically and sometimes horizontally, and the small round seeds fly 6 feet or more. Lubbock records a distance of nearly 20 feet. When the fruit is ripe, a mere touch sends it off, and a passing animal touching it would probably receive the seeds on its abdomen or sides, where it would adhere from the mucilage. It is possible that the plant reached the Azores by adhesion of the seeds to the plumage of some bird, but more probably in ballast (Pl. XXII, fig. 21).

Cyclanthera explodens is an annual gourd (*Cucurbitaceae*) of Ecuador and New Grenada. It is scandent, with a gibbous curved fruit, spiny on the back, 1½ inches long, green, turning slightly yellow when ripe, and hardly succulent. It contains about 8 seeds, flattened and lobed. On maturity it splits spontaneously, or, if very slightly touched, into 3 lobes, which recurve elastically, throwing out the seeds. The placenta remains attached to the middle lobe. *Momordica charantia* splits in a similar way, but the seeds are enclosed in a red aril attractive to birds, and thus are not ejected.

Lathraea clandestina (*Orobanchaceae*).—This dwarf plant, which is quite sunk in the ground, is a native of Southern Europe, and parasitic on Beech, Elm, Hazel, Lilac, Privet, Euonymus, Alder and Rhododendron. The capsules are ⅓ inch long, obconic, with flattened sides. Each contains 2 or 4 seeds. When the fruit, which is almost immersed in the ground, is ripe, it explodes on a dry day or when pressed, throwing the seed to a considerable distance. J. L. North (*Quart. Rep. Bot. Soc.*, 1924) records the flight of a seed as far as 72 feet, but the average is somewhat less. Druce (in the *Report of the Botanic Society*, 1925) found specimens as far as 40 feet away from the place where it had been planted by Lady Saumarez some years previously. *L. squamaria* has a tall stem, and the capsules do not explode. They dehisce gradually from the top, and let the seeds fall out spontaneously, to be dispersed by rain-wash.

The explosion of the pods of some of the *Leguminosae* is known to everyone, as, on the open heaths on all hot summer days, the crackling of the exploding pods of the gorse and broom can be heard distinctly. The 2 valves of the pods, when dry by the heat of the sun, separate suddenly so as to eject the seeds to some distance. In some cases, *Ulex*, *Cytisus*, *Wistaria*, etc., the valves merely separate and spread; but in many plants, after dehiscence, the

pod-valves twist up spirally, e.g., *Lotus*, *Bauhinia*. This explosion is effected by a hard layer of strongly thickened elongate cells which runs transversely across the valve, and which winds into a spiral when drying. The softer cells give practically no resistance, so that, when the twist of the valve takes place, it is very sudden. The force of the projection varies according to the thickness of the wall of the valve. The distance to which the seeds fly therefore varies in different fruits.

In the smaller-fruited *Papilionaceae*, like *Ulex* and *Sarothamnus*, Gorse and Broom, the flight is only a few feet, enough, however, to throw the seed clear of the bush. Kerner gives the distance of flight of the seeds of *Dorycnium decumbens* as 3 feet only. R. Rangachari says that those of *Canavalia*, in which the pod merely expands suddenly and does not twist, are hurled to a distance of from 10 to 18 feet. The seeds of *Lupinus digitatus* are stated to fly 21 feet, but I found those of *L. arboreus* to go about 2 feet only, and of *Cytisus Laburnum* about 6 feet, from the tree. According to Kerner, those of the treelet *Bauhinia purpurea* go as far as 40 feet. Under the heading of " A Plant Catapult," Halsted gives an account of the violent explosion of the pods of the stout climber, *Wistaria sinensis*.—The seeds are flat on one side and rounded on the other, and, on dehiscence of the pod, flew 10 feet across a room, striking the window violently, and he calculated that, had the window been open, they would have gone 15 feet; and Zabriski says that the pods (of which he gives a figure) split to the base and turn outwards, not twisting spirally. They threw the seeds hard against a window 16 feet away, and rebounded for 4 feet, so that he judges they would have gone 30 feet in the open.

The spiral torsion of the valves in many cases appears to me to be a disadvantage to the plant. It certainly expels most of the seed, but I observed in *Lupinus arboreus*, where the valves twisted up very tight, that the seeds, which were detached at the separation of the valves before the spiral torsion took place, flew away satisfactorily; but any which did not escape then were held tight in the spiral, and could not escape, and I have seen this in other species (Pl. XXII, figs. 1 and 2, *Lotus corniculatus*).

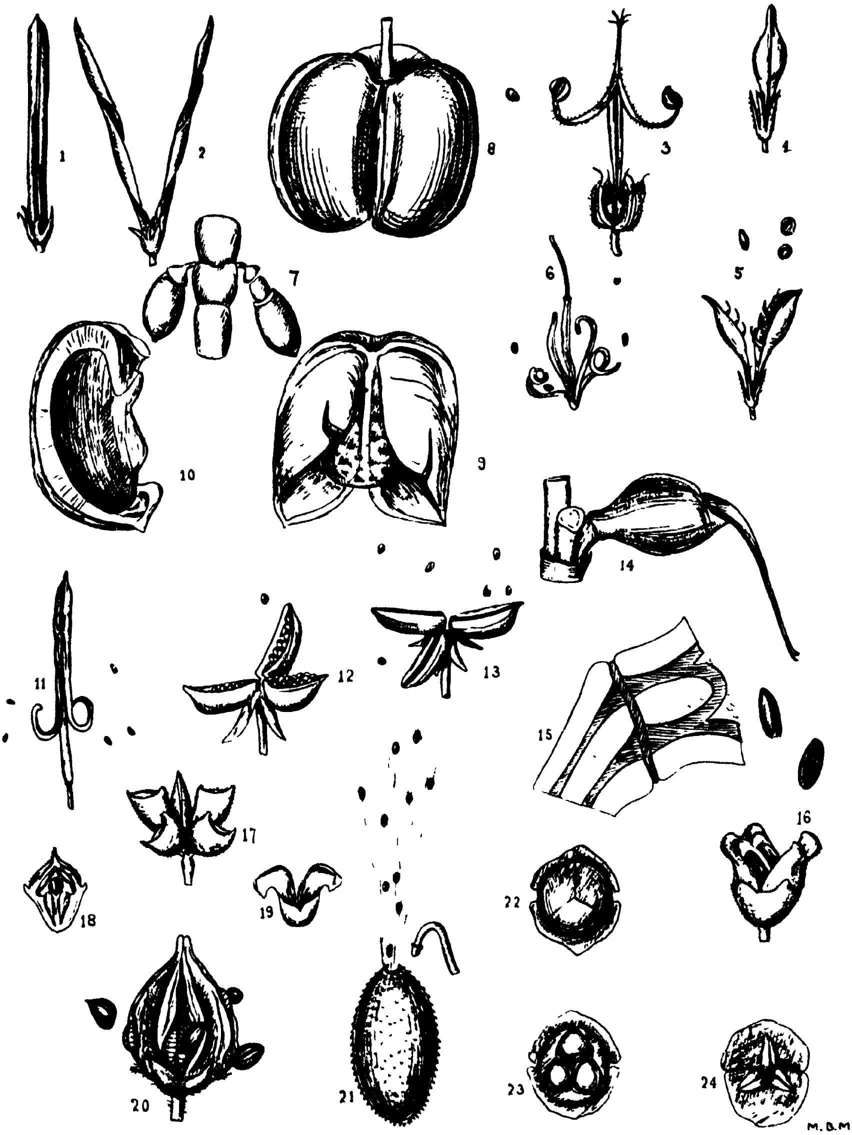
The explosion and torsion of the pod are characteristic of many of the herbaceous and shrubby *Papilionaceae*, especially the sections *Viciae* and *Phaseolae*, and also occurs in *Bauhinia*, trees and lofty climbers of the tropics. In most cases of the smaller plants the seeds are further dispersed by rain-wash or ants.

Spiral torsion of the pod is also met with in some of the *Gesneraceae*, viz., *Boea* and *Streptocarpus*. The former herbs are usually inhabitants of limestone rocks, and apparently fruit in the dry season, when the whole plant dries up, recovering again in the rainy season. The pod or capsule is narrow and linear, with numerous minute seeds. In the allied plants, *Paraboea* and *Didymocarpus*, which inhabit permanently wet localities in Malayan and Indian forests, the pod opens along the upper edge and the seeds are dispersed by rain-wash.

As there is no rain during the season in which the pod of *Boea* is ripe, I presume the seeds are ejected, as in the *Leguminosae*, by the spiral torsion of the valves, so as to be thrown clear of the mother-plant. *Streptocarpus* has the same method of dehiscence. The genus is African, with 1 Siamese and 1 Chinese species (which, however, I doubt belong to the same genus). In some of the African species the plants are described as growing on rocks by streams, and one is epiphytic on trunks of trees in wet forests. However, so little has been recorded as to the habits and natural history of these plants, that I cannot give any reason for the spiral torsion of the pods.

In almost all the plants of the order *Acanthaceae* the seeds are dispersed by explosion of the capsule. In fact, this method of dispersal, and the adaptations for it, are the main distinguishing characters of the order. The plants are

PLATE XXII.



EXPLOSIVE FRUITS.

FIG. 1.—*Lotus corniculatus* (pod).
" 2.— " " (after dehiscence).
" 3.—*Geranium pratense* (fruit).
" 4.—*Ruellia prostrata* (fruit).
" 5.— " " (" after dehiscence).
" 6. *Impatiens noli-me-tangere* (fruit dehiscing).
" 7. *Arceuthobium pusillum* (fruits, enlarged).
" 8.—*Hevea braziliensis* (fruit).
" 9.— " " (single carpel and seed).
" 10.— " " (empty loculus).
" 11.—*Cardamine impatiens* (dehiscing).
" 12 and 13.—*Viola elatior* (capsules dehiscing)
" 14.—*Polygonum virginianum* (fruit).

FIG. 15.—*Polygonum Virginianum* (section through fruit attachment, after Reed and Schmoot).
" 16.—*Hamamelis mollis* (capsule dehiscing).
" 17.—*Dictamnus albus* (fruit).
" 18.— " " (carpel with seed).
" 19.— " " (endocarp after dehiscence).
" 20.—*Oxalis acetosella* (capsule dehiscing).
" 21.—*Ecballium elaterium* (fruit dehiscing).
" 22.—*Claytonia alsinoides* (fruit).
" 23.— " " (valves dehiscing).
" 24.— " " (after discharge of seeds, enlarged, after Willis.)

[*To face p.* 666.

herbs, seldom climbers or shrubs, chiefly growing in open country, or on the borders of forests, or in open spaces in woods, and are chiefly tropical, occurring in the tropics of both worlds, and moving into subtropical regions as far north as Southern Europe (*Acanthus*). The few that occur in oceanic islands usually have adaptations in the bracts or the seed for adhesion to birds, or are sea-borne.

The capsules are woody in most cases, and 2-valved, containing 2 or 4 seeds, occasionally more. The seeds are generally discoid and flat, and the funicle becomes woody during ripening (retinaculum), and is curved. When the fruit is mature, the valves suddenly separate, the retinaculum, previously more or less depressed, springs up and slings the seed to a distance. In many species the base of the capsule is solid, and this appears, in dehiscing, to add to the jerk given to the seed (Pl. XXII, figs. 4 and 5, *Ruellia prostrata*).

In *Acanthus longifolius* I find the seed flies about 23 feet. Kerner records the flight of those of *A. mollis* to be 9·5 metres (about 28 feet). R. Rangachari states that in *Ruellia prostrata* the fruits have at the tip a specialised spot which, when wetted, leads to the splitting of the capsule and the discharge of the seeds in all directions.

C. E. B. Bremekamp (in the "Opening Mechanism of the Acanthaceous Fruits," *South African Journ. Sci.*, xxiii, 408) says the top of the pod consists mainly of sclerenchymatous cells which, when dry, adhere in a mass, but when wet they are easily separated. In water the middle lamellae of the cells begin to swell, and the force which binds these cells together gradually decreases, so that the ripe fruits, when wet, do explode. He points out that the seeds of all *Acanthaceae* are somewhat sticky when wetted.

In *Blepharis boerhaaviaefolia*, in which the seeds are dispersed by the adhesion of the calyx to the fur of animals, the capsule is shorter than the calyx, and does not dehisce explosively, but splits in the calyx, the seeds being dropped out by the animal, to which the calyx adheres as it walks along. Here explosive dehiscence would actually be useless, and interfere with the adopted method of dispersal.

Dictamnus fraxinella (*Rutaceae*).—This plant has another type of explosive capsule. It is a tall herb, native of open pastures or mountain slopes in Europe and temperate Asia as far as Japan, with a spike of somewhat woody or cartilaginous fruits of 5 carpels spreading in a star about ½ inch long, and splitting along the upper edge. After dehiscence the free endocarp, stiffly cartilaginous, splits along the upper line, but for some time remains connate in 2 linear-oblong lobes still containing 3 pear-shaped, black, smooth, polished seeds. The basal part then twists suddenly and separates completely into 2 parts, ejecting the seeds to a distance of from 3 to 6 feet, the 2 lobes of the endocarp flying out at the same time. This sudden twisting or convolution of the inner edge is much like the twisting of the leguminous pod, or perhaps more like that of the Euphorbiaceous capsule (Pl. XXII, figs. 17, 18, 19).

Much the same system is adopted in the tree and shrub species of *Evodia*, *Melicope*, and *Boninia*, but in these the carpels are much smaller, and contain each a single seed, round, black, smooth and polished. In the allied genera *Zanthoxylon*, *Astrophyllum*, and *Terminthodia*, the endocarp separates from the exocarp, but does not become twisted, nor does it eject the seed, which, in *Zanthoxylon*, is smooth and polished, but seems only to be pressed out of the follicle by its drying and contracting. In *Terminthodia* the seeds are winged and flat, and dispersed by wind. They are low bushy shrubs found on mountains in the Malay Peninsula and New Guinea. *Evodia* and *Melicope* are Asiatic trees and shrubs, sometimes of considerable height. I have never seen their seeds expelled as violently as in *Dictamnus*, but the endocarp is certainly incurved and twisted as in that plant.

A somewhat similar method is found in *Colubrina ferruginea*, a West Indian shrub, which is thus described by W. Fawcett (in the "Flora of Jamaica," vol. v, p. 68):—"The seeds are shot out by dehiscence of the cocci. The "lower halves of the side-wall of the cocci are thinly membranous, and "separate somewhat in the form of a valve bending outwards, and thus "separating the cocci. Suddenly the splitting along the inner angle of the "cocci extends upwards towards the apex and about halfway down the endo-"carp, and the seed is shot several feet away."

Colubrina belongs to the order *Rhamnaceae*, and is confined to the New World, except for one species (and one or two derivatives), *C. asiatica*, which is widely dispersed by sea over the Old World. None of the other species disseminate their seeds in the same way as *C. ferruginea*, so far as I know.

Phlox Drummondi (*Polemoniaceae*).—This little American plant, so common in gardens, has an oblong capsule about ¼ inch long, containing 3 seeds. When ripe, it is pushed up by contraction of the calyx, and splits suddenly along the lines of the 3 valves, ejecting the seed, which fly with some violence to a distance of 3 feet (Halsted, in *Torreya*, i, 1901, p. 143).

In *Collomia*, e.g., *C. grandiflora*, the same principle is utilised, only that the capsule is distinctly 3-lobed, and the calyx does not appear to contract and push up the fruit. In the Phlox the 3 cocci split into 2 valves each, and are slightly twisted in dehiscence, so as to throw the seeds out, there being 1 seed in each coccus. I find in different flowers that though the number of cocci is normally 3, many flowers develop only 2, and sometimes but 1, suggesting an evolution towards a single-seeded capsule like that of *Phlox paniculata*. In this tall Phlox of our gardens the ovules of 2 of the 3 cells do not develop, so that the fruit is 1-seeded, and does not dehisce. In fact, it may be said to be a kind of dry drupe, and the only method of dispersal is due to blasts of wind shaking the tall stems, and, later, the transport of seeds away from the plant by rain-wash. In most of the species of the genus, however, the capsules do dehisce, as in *Ph. Drummondi*.

Another genus of plants which have a somewhat similar method of dispersal is *Hamamelis* (*Hamamelidaceae*), the Witch-hazels of North America, China, and Japan. They are fairly large bushes, with capsular explosive fruits. Of *H. virginica*, of North America, Meehan gives an account. In this plant the woody capsule is enclosed at the base in the cupular calyx. It is formed of 2 valves, which split at the top when dry, very suddenly, exposing 2 black seeds in each valve; as the fruit dries, the endocarp contracts, shooting out the seeds with great violence. Meehan states that they strike people violently in the face as they pass through the woods where the Witch-hazel bushes grow. He records the distance of the flight of the seeds as from 4 to 6, and some as much as 12 feet. Gleason ("Dispersal of Seeds," *Journ. New York Bot. Gard.*, xxxvi, 1925, 232), says the Witch-hazel has pods which soon open, and show the ends of 2 hard black seeds. As the pods get drier, they begin to shrink, and exert a considerable pressure on the seeds, until they are discharged, like miniature bullets, to a distance of 40 feet. Miss Bessie Putnam records their flight distance as 17 feet. In *H. mollis*, of China, fruits of which I received from a Surrey garden, the capsule was ½ inch long, and, when dry, suddenly separated at the top, each cell also splitting, and ejected the seeds with great violence. The seed is elliptic, smooth, black and polished, slightly pointed at the upper end, a little over ¼ inch long. The endocarp did not seem to contract at all, but apparently the whole wall of the carpel did simultaneously with its dehiscence. I could not estimate the distance of flight, but the explosion was a very violent one (Pl. XXII, fig. 16).

Viola.—A number of species of Violets possess explosive capsules by which the seeds are shot to some distance, but by no means all are thus dispersed. *V. elatior*, of North America, *V. canina*, of Europe, *V. serpens*, *V. reniformis*,

V. Patrinii, of India, have this means of dissemination, which is not possessed by *V. odorata*, *V. hirta*, etc. The fruits are capsules of 3 valves, which are boat-shaped, with thin margins and a broad keel. A cross-section of the valve shows a layer of thin-walled parenchymatous cells, a layer of elongate curvilinear ones, and a layer of broad thickened cells. The unequal drying up of these layers causes the curving up of the sides of the valves, which force out the seed. The terminal seeds of the first carpel (valve) are ejected first, and the basal ones last. When the first carpel is empty, the next begins, and when it has finished, the third commences (Kerner) (Pl. XXII, figs. 12 and 13).

R. G. Leavitt (*Rhodora*, 1902, 183) gives an account of *V. rotundifolia*, of North America. He states that the middle row of seeds (of the 3 rows in the valves) go first, some being merely pushed out, and some fly less than a foot distance; those caught in the jaws of the machine, or have the strongest attachment to the placenta, go farthest. After coming to rest, the seeds are further dispersed by rain-wash.

The distances to which the seeds of Violets are thrown by the explosion of the capsule seem to vary a good deal. Ulbrich quotes Gross as to the distances of flight of several species :—

Viola canina	from 2·68 to 4·72 metres	—	approx. 8	to 15 feet.
V. elatior ..	,, 1·75 to 4·65 ,,	—	,, 5·6	to 15 ,,
V. sylvestris	,, 0·20 to 3·75 ,,	—	,, 8 ins.	to 12 ,,
V. Riviniana	,, 1·83 to 4·63 ,,	—	,, 5·9	to 15 ,,
V. rupestris..	,, 0·70 to 3·80 ,,	—	,, 1·8	to 12 ,,

Leavitt gives that of *V. rotundifolia*, of America, as certainly 5, and probably 9 feet. Beal (in *Rhodora*, 1902, 230) says that *V. alpestris* shoots its seeds in every direction as much as 10 feet. Kerner gives the flight of the seeds of *V. canina* as 3 feet, but Nowers has seen them go as far as 10 feet across the room, so we may reckon that about 15 feet is as far as these seeds are thrown. On hill slopes and such spots they might roll a good deal farther.

The capsules of some of the species of *Alsodeia*, shrubs of the order *Violaceae*, much resemble those of the explosive *Violas*. The seeds are globular, but fewer in each valve of the capsule, and are also larger. They are probably ejected in the same way, but I have not seen the dehiscence. The plants are shrubs or treelets of tropical Asia and South America. Apparently the same principle is employed in the remarkable Anonaceous tree *Anaxagorea*. Unlike any other plant in the order, the separate carpels are of a flattened club shape, about ¾ inch long; the upper portion, containing 1 or 2 flat, polished, slippery seeds, is nearly ½ inch long, and bent at an angle. It splits along the upper line, and the seed is forced out. The genus has a remarkable distribution, being found in the Malay region and Trinidad. The species inhabit dense wet jungle.

Claytonia (*Portulacaceae*).—Willis (in *Ann. Bot.*, vi, 382) figures and describes the fruit and explosive dehiscence of the small plants *Claytonia alsinoides* and *C. sibirica*. In these dwarf herbs the peduncle of the flower, at first erect, bends down, and again becomes erect when the fruit is ripe. The fruit is a small oval or spherical capsule which contains 3 seeds. It splits loculicidally into 3 valves, the seeds now forming a triangle, one across each of the slits between the valves. The seeds are ovoid, polished, and slippery. The valves fall back after dehiscence till the seeds are fully exposed, and, as they become dry, the sides move inwards towards each other, as in the violet capsule. The effect is to press the seeds tightly together until the resistance to slipping caused by the slightly tubercular surface is overcome. Then 1 (probably the one which stands highest) is shot out, and sometimes 2, and sometimes all 3 simultaneously. The distance to which the seeds fly is from 1 metre (3 feet 3 inches) to 1½ metres (nearly 5 feet) (Pl. XXII, figs. 22 to 24).

Cl. perfoliata I have examined, as it is abundant in open soil in beds in Kew Gardens. The capsule, which is $\frac{1}{8}$ inch across, is globose, and the seeds flattened, oval, black, and polished. The dissemination takes place as is described by Willis in the other two species above. The seeds are shot out singly to a distance of about 3 feet, but probably frequently go farther than this, as the plants are to be found scattered far apart. The flowers in this species are pedicelled, but sunk in the saucer-like perfoliate leaf, so that, if merely dropped after dehiscing, the seeds would not be dispersed.

The same system of dissemination is found in the small herb *Montia fontana*, which is very widely dispersed all over the temperate regions, including the Antarctic islands, where it is evidently transported on the feet of birds. The capsules are very small, and, according to Ulbrich, on their dehiscence the seeds fly to a distance of 60 cm. (2 feet) to 2 metres (6 feet 6 inches). Urban figures and describes the explosive system of this plant in a paper "Ueber die Schleudereinrichtung, bei *Montia minor*" (*Jahrbuch Konigl. Bot. Gard. Berlin*, iv, 1886, p. 256, pl. ii, figs. 15-22). The seeds are papillose, and the capsule valves, though similar to those of *Claytonia*, after dehiscence and ejection of the seeds, roll up spirally.

In the large order of *Euphorbiaceae* those species which have capsular fruit very frequently have an explosive mechanism. The carpels are generally 3 in number, connate in the centre, each of them containing a more or less oblong seed. The outer layer of the pericarp is thin and soft, and soon becomes dry, the inner endocarp is hard and woody, composed of transverse fibres which are straight when wet, but recurve on themselves when dry, so suddenly as to cause an explosion and eject the seed. Dandeno, in an account of the explosion of the Castor-oil fruit (*Ricinus communis*), points out that the position of the fruit on the plant is at an angle of 45° to the horizon, the best angle theoretically for the flight of the seed. This is not, however, by any means always the case in other *Euphorbiaceae*; thus in the Para rubber (*Hevea*) the fruit hangs downwards towards the ground, and in many genera the fruit is axillary. In *Ricinus* they are borne on an erect peduncle at the top of the plant.

In *Hevea braziliensis* the large green fruit becomes dry when ripe. The carpels detach themselves first from the central columella, and then from each other. The dorsal wall contracts with increasing pressure, till the carpel gives way at the top, its weakest point, first splitting septicidally; then each carpel splits of itself loculicidally, slightly twisting, and ejects the large seed with some violence. Frequently the two dehiscences take place almost simultaneously, but usually the carpels separate first, followed, after a very short but appreciable time, by the loculicidal dehiscence of the woody endocarp (Pl. XXII, figs. 8, 9 and 10).

In gathering the fruits of *Hevea braziliensis* with a long hook from the high trees, the carpels would separate when touched and split violently before reaching the ground. In a plantation, when the fruit is ripe, in the sunny part of the day the popping of the capsules can be heard continuously. The capsule is round, 3-lobed (normally, but trees producing bicarpellary and 4-carpellary fruits are not unknown), green, about 3 inches across.

When ripe, the outer layer becomes yellowish before dehiscence. The large, oblong, rounded seeds, about 1 inch long, fly from the trees as much as 40 yards. Should they, on falling, strike a stone, piece of wood, or hard ground, they bound often 2 or 3 times, till they reach a soft spot or water. When they strike soft mud, they bury themselves in a sloping direction for half their length, the position in which it is found most satisfactory to plant the seed. The seeds float in water, and as in the Amazons forests it is largely a river-bank tree, the seeds are readily further dispersed by water. The brown

colour with silvery markings in *Ricinus*, *Hevea*, etc., are not intended to cause the seed to resemble a beetle, as suggested by Lubbock and others, but rather to make the seed less conspicuous, the silvery patches suggesting light flecking the ground. The seeds of *Hevea* are greedily devoured by wild pigs, rodents, and other animals, and the wide scattering and their almost cryptic colouring serve to protect them from destruction by these animals.

As Kerner points out, the larger the seed, the farther it flies, and naturally the fruits of the big trees like *Hevea*, *Hura*, *Elateriospermum*, which have big seeds, send them farther than those of dwarf herbs like *Euphorbia* and *Mercurialis*. As mentioned, *Hevea* seeds will fly from a big tree 40 yards. Kerner gives the distance to which *Hura crepitans* throws its seeds as 14 metres (42 feet), but it probably goes farther than that in a wild state. Dandeno gives 3·65 metres (about 11 feet) as the flight of Castor-oil seeds (*Ricinus*). Schenck, in describing the explosion of fruits of *Euphorbia marginata* (*Bot. Gaz.*, 1887, p. 228), says the seeds fly 12 feet, and S. J. Mukerji (*Journ. Bot.*, 1927, p. 56), in describing *Mercurialis perennis* var. *salisburgensis*, says the ripe fruits burst open and eject the seeds to a distance of about 4 metres (13 feet). This seems to be the usual distance to which the small capsules of these low herbs throw their seeds.

The genus *Buttneria* (*Sterculiaceae*) possesses explosive capsules so closely resembling those of some species of *Mallotus* (*Euphorbiaceae*) that botanists have mistaken fruiting specimens for those of some plant of that genus. The plants are climbers, erect shrubs, or small trees, found in Africa, tropical Asia, as far north as China, and Central and South America. The capsule in such a plant as *B. Maingayi*, a native of tropical Asia, is globose, 1½ inches long, and spiny, containing 5 woody cells, which, in dehiscing, separate from the columella, and split again down the inner face, and discharge a single seed each. The cocci separate widely, and become often slightly twisted. According to a note on *B. Jackiana*, apparently in W. Hooker's handwriting, the cocci separate and again are separated into 2 valves, bursting with considerable report in a dry room.

Alstroemeria (*Amaryllidaceae*) is a genus of herbs about 2 feet tall, growing in open countries in South America. The fruits are capsules borne on the top of the plant and standing erect. They are globose and ½ inch long, of 3 boat-shaped valves, and contain about 10 seeds each. The seeds are round, papillose, and about ¼ inch long. When ripe, the capsule, whether touched or not, explodes suddenly with a distinct report, and the valves fly away to a distance of about 2 feet; at the same time the woody placentas, 1 on each valve, spring up much as the retinaculum of the *Acanthaceous* capsule does, and hurl the seeds away. The placenta becomes detached from the base of the valve, but remains attached to the top. The seeds (in all I have seen) fly to a distance of from 6 to 10 feet, but Stapf gives the flight of those of *A. psittacina* as 4 metres (13 feet). The plants usually grow in clumps, which is, perhaps, the reason for the requirement of an explosive mechanism.

The discharge of the seed of the *Geraniums* is effected by a very different mechanism from that of other plants. The carpels are 5 in number, each containing a single seed. They are dilated at the base, where the seed is, and prolonged into slender linear processes, which, with the style, form the crane's bill. When ripe, the tissue of the beak dries, and the outer layer, being succulent, dries faster than the inner layer of thick-walled cells, causing the carpellary beak to coil up like a watch-spring. The cavity of the carpel being open on the inside, and carrying the seed loose, as it were, in a spoon, on this sudden contraction the seed is thrown into the air, as from a sling, to some distance. The tops of the carpellary beaks remain attached to the axis.

In *Geranium Robertianum*, the Herb Robert, the seeds are often thrown

20 feet away, and I have seen the plant growing on roofs quite 12 feet from the ground. The gutter of my greenhouse, 6 feet from the ground, was filled one year with seedlings, the seeds having been thrown from the ground to the sloping glass roof and rolled down into the gutter. The plant seems to spread with remarkably rapidity. The genus is abundant all over the temperate regions, and occurs in tropical mountains. *Erodium*, similarly dispersed, is almost as widely distributed, and *Pelargonium* is abundantly represented in Africa (Pl. XXII, fig. 3, *Geranium pratense*).

The dissemination of the achenes of the North American *Polygonum virginianum* is effected by a remarkable mechanism described and figured by H. S. Reed and I. Smoot (in the *Bull. Torrey Club*, 88, 1906, p. 377). The plant is a simple stemmed slender herb about 2 feet tall, with a long graceful terminal raceme of small scattered flowers. The fruit is an achene, bearing on the tip a long, persistent, 2-partite style, which becomes lignified and hooked when the achene is ripe. If, when mature, these styles are struck sufficiently hard, the achenes are thrown off to a distance of 9 to 13 feet. During windy weather the tall slender racemes are blown together and against the strong stems of plants like *Phytolacca* and *Sambucus*, with which it associates.

Passing animals also act as disseminators, for, if they strike it with enough force, the achenes are thrown with sufficient violence to cling to fur or fleece by the sharp reflexed style-points.

The mechanism by which this is effected is as follows: below the achene in the pedicel there is a separation layer developed at a very early stage. The fibro-vascular system may be compared to a thin-walled inelastic cylinder, inside which the elongating pith-cells act like a piston moving against the soft spongy pith-cells in the closed end of the rigid cylinder. The cushion of thin-walled cells is like a compressed spring, the end of which presses against the achene and against the separation layer. So long as the structure is undisturbed, the fibro-vascular cylinder restrains the elongating force of the pith column, but when the achene is struck sufficiently hard, the strained walls of the cylinder break at the separation layer, and the compressed cushion of cells, suddenly expanding like a released spring, throws the achenes off with considerable force (Pl. XXII, fig. 14 and 15).

Circaea alpina.—Dr. H. Christ (in " Projection des fruits chez *Circaea alpina*," *Bull. Geogr. Bot.*, xxii, 1912, p. 245) says that he has observed that the fruits of *Circaea alpina* are violently thrown to a distance, being abruptly separated from the " petiole " (evidently a misprint for pedicel), but he was unable to find out how this was effected. The fruits of *C. alpina* are smaller and more obovate than those of *C. lutetiana*, but still bear some hooked bristles. Inhabiting mountain districts where animals which could transport its armed fruits are rare, it might well have adopted another method of dispersal. The plant ranges over the whole temperate region in mountain districts, as far south as Siam in Asia. It would be very interesting to have Dr. Christ's account of its dispersal in this way confirmed for other districts, and to find out how it is effected. I examined living plants in Kew Gardens, but, unfortunately, they did not set fruit in 1928, and I can see nothing in the dried specimens to confirm Dr. Christ's account.

The small parasitic mistletoes, *Arceuthobium* (*Razoumoffskya*), are parasitic on the branches of various coniferous plants, *Pinus*, *Larix*, *Juniperus*, etc., in the north temperate zone, chiefly in North America and Mexico. One species, *A. oxycedri*, parasitic on Juniper, occurs in Southern Europe, Algeria, Armenia, to the Himalayas, Azores, Africa, Mount Kenya, and North America. Another species occurs on the Himalayas, and 1 in China.

The species are remarkable for their explosive 1-seeded fruit. These little drupes are, when ripe, borne on a short pedicel, from which they hang

downwards. The pericarp consists of an epidermis, beneath which is a mass of parenchymatous cells, and below, a fibro-vascular system, and underneath that an expulsion layer of long thin-walled cells arranged to force out the seed. Towards the base of the drupe there is a scission layer. When the expulsive layer of cells has absorbed a sufficient quantity of water, the drupe breaks through at the scission layer, and the seed (which is of the shape of a rifle-bullet, conical at the basal end and truncate at the apical end) is shot out with considerable force. The seed is morphologically a seed enclosed in the inner part of the ovary. The greater part of it is covered with a gelatinous layer, sticky enough to attach it to anything rough or smooth (Pierce, "Dissemination and Germination of *Arceuthobium occidentale*," *Ann. Bot.* xix, 99; Jack, "*Arceuthobium pusillum*, Massachusetts," *Rhodora*, ii, 13, p. 6).

Reinaud de Fonvert (in "Note sur *Arceuthobium oxycedri*," *Ann. Nat. Sci.*, ser. iii, vi, p. 129) gives much the same description of the explosion of the European species, but says that, when the seed flies out, it carries with it the viscous part of the umbilical cord. The explosions of the ripe fruit are increased in number if the branches are shaken or struck, and Piper ("Flora of the State of Washington, U.S.A.," Nat. Herb., ii, 1906, 222) says that from the noise of the exploding fruit *A. californica* is known as "Snappers." Pierce says of *A.* (R.) *occidentale*: "Without any apparent disturbance, the "fruits would explode. I could hear them. I might even be struck by the "flying seeds, but if the wind gently shook a bunch of fruiting *Arceuthobium*, "or the raindrops fell on the fruit, or I lightly struck a branch of pine on which "the fruiting parasite grew, there would be a momentary fusillade."

The distances to which these seeds will go is variously given for different species. Reinaud de Fonvert says that those of *A. oxycedri* fly to the distance of a metre (3 feet 3 inches). MacDougal says of *A. robusta*, they fly 2 to 3 metres (6 to 9 feet). Pierce says of *A. occidentale*, the longest distance was 15 feet in the laboratory, but he had no doubt it could have gone 10 feet farther. J. R. Weir (*U.S.A. Bull. Agric.* 360, 1916) says of *A. Douglasii*: "It has been shown that seeds expelled at a height of 8 feet will go over 66 feet, "and in one instance seeds were collected in large numbers from the roof of "a cabin ¼ mile from the tree." This is the longest flight of any seed ejected by explosion, and seems almost incredible.

According to H. Schrenk, birds sometimes transport the seeds of these plants from one tree to another, and, indeed, a bird alighting on a tree bearing the plant in fruit might well get covered with the viscous seeds. He says it must have been in this way (for instance) that the plant was conveyed to Monhegan Island, where it was found. Probably also the species found in San Domingo by Urban was bird-borne, and this must certainly have been the case in the Azores, where Guppy found the *Arceuthobium oxycedri* of Europe growing on the Juniper bushes. This method of combined dissemination by explosion and adhesion is also believed to occur in the case of *Ecballium*, where the seeds are shot out in a mass of viscous mucilage (Pl. XXII, fig. 7).

Dorstenia (*Urticaceae*).—This is a genus of herbs or shrublets, mostly found in South America and Africa, with 1 Indian species. The inflorescence consists of a concave receptacle, round, square, or variously lobed, or drawn out into 2 or 3 narrow limbs, borne on an erect peduncle, and carrying on the upper surface a large number of minute flowers sunk in the fleshy mass. The walls of the pits, in which are the flowers, are composed of the fleshy calyces. When the very small achenes are ripe, the whole receptacle dries up and shrinks, so that they are shot out by the pressure, away from the plant.

A somewhat similar principle is employed in the big tree *Sloetia sideroxylon*, a native of the Malayan forests. In this the receptacle is linear, and covered on one side with many male and a few larger female flowers. The achene,

when ripe, is pea-shaped, globose, and smooth, and is gripped by the succulent white, much-swollen 2-lipped calyx. As this swells, the achene is suddenly shot out either by the natural pressure, or by a bird feeding on the fleshy calyx, the compression of whose beak is sufficient to cause the flight of the achene. The calyx is really 4-lobed, but only 2 of the lobes swell and eject the achene. The actual flight of the fruit seems to be only a yard or two, but as it is rounded it may roll further.

Fungus Spores and Sporanges Discharged by Explosion.

In the *Ascomycetes*, *Peziza*, etc., the ascospores are shot out of the asci with some violence when ripe, spontaneously, or, on being touched, the lid of the ascus flies off and the 8 spores are ejected. Several suggestions have been made for the explosion, including the withdrawal of the water, but no very satisfactory reason has been given.

Ascobolus immersus shoots its spores to a distance of 15 feet. They are distributed on grass or other herbage, and eaten by horses and cattle, germinating in the excreta. *Empusa muscae*, parasitic on the fly, can distribute its spores 1 or 2 inches away; *Hymenomycetes* spores can only fly by extrusion 0·01 to 0·02 cm.

The asci of *Ascobolus immersus* are projecting, and, being heliotropic, point always towards the light—that is to say, in Nature towards open spaces, and away from the excreta on which they are growing (A. H. R. Butler, "Researches on Fungi").

Pilobolus shoots away its whole sporange to some feet distance. The gun (*ascus*) which effects this consists of a basal reservoir, at first densely filled with protoplasm, and fixed at the base by rhizoids, a slender stipe, and a large terminal oval sub-sporangial swelling, on the top of which is a discoid sporange. The neck of the sub-sporangial swelling is ruptured transversely, and its walls, and those of the stipe, contract elastically, and the sap squirts out of the top. The sporanges, which are very adhesive and stick firmly to herbage, fly to a height of 6 feet and a horizontal distance of 8 feet. The sub-sporangial portion turns towards the light, so that the sporanges fly to a clear place.

In *Sphaerobolus* the flight of the sporanges is even farther than this. The fruits are spherical and 2 or 3 mm. through. Embedded in the mycelium, when ripe the outer parts of the fruit-bodies break open in a stellate manner in the early morning; later in the day a clear watery liquid accumulates round the glebal mass, and a rupture takes place in the two layers of the peridium, the inner layer suddenly inverts and throws the glebal mass of spores to a distance of 14 feet (L. B. Walker and E. N. Anderson, "Mycologia," xvii, p. 134).

Propulsion of Bulbils.

F. E. Lloyd (*Torreya*, ii, 177) and Leavitt (in *Rhodora*, iv, 57) give an account of the propulsion to a distance of the gemmae or bulbils of *Lycopodium lucidulum*, in Massachusetts, North America. The gemmae in the leaf-axils are, on the stems being touched, shot out to a distance of from 4 or 6 inches to 3 feet or more. Leavitt found seedlings growing at a distance of 3 feet from the parent plant and 1 foot above it. He bent the cotyledon-like leaf of one of the buds, and the gemma (bulbil) flew off 11 inches, and another 25 inches. If struck by passing birds or rabbits, or perhaps even by raindrops, they might fly as much as 3 or 4 feet away.

CHAPTER XI

ISLAND FLORAS

• Notes on Various Islands.

ISLANDS may be separated into two classes, the CONTINENTAL ones, which are really detached fragments of a mainland or larger island, and OCEANIC or free islands, which have had no previous land connections from which the flora now existing on them could be derived. CONTINENTAL islands are characterised, in the method of the flora, in possessing a much larger number of species than those on OCEANIC islands, and further in that the number of species in different genera is larger, and we usually find a certain number of plants which we know have no facility for crossing the sea to the required distance.

In oceanic islands the number of species possessed depends largely on the distance from the nearest land, as well as, to some extent, the soil and conditions of the island. The genera, of flowering plants at least, are usually represented by 1, more rarely 2 species, very seldom more. Many of the smaller and more remote islands, such as Cocos-Keeling and Diego Garcia, have a flora consisting almost entirely of sea-borne plants, with a few borne adhesively by sea-birds, and some of human introduction.

As we know now approximately all the methods of seed-dispersal, we are enabled to say definitely that the occurrence of certain types of plants in any island is strong evidence that the island must have been formerly attached to a mainland, or these plants could never be found there. Thus in the Canary Islands we find an endemic Fir tree (*Pinus canariensis*), and an Oak, a form of *Quercus lusitanica*, the parasitic *Cytinus*, and some other plants which could not have crossed even a few miles of sea, and must have come overland, showing a former mainland connection. Such plants are absent from the oceanic Azores. The animals inhabiting islands also give corroborative evidence. The land-tortoises and snake of Galapagos, the freshwater fishes of Kerguelen, the occurrence of batrachians on an island, all form strong evidence that these islands were formerly attached to a more extensive land, and that the accompanying flora, for the greater part at least, arrived at the time of the previous mainland connection.

The flora of an isolated piece of land may have been destroyed by a catastrophe, and the island repopulated by a new flora. It is improbable that Krakatau is the only island where this has occurred. Dead timber representing previous forests has been found in Kerguelen, probably destroyed by a Glacial period. Glaciation, volcanic eruption, or the emission of volcanic gases (as has happened in parts of Hawaii), might cause the complete destruction of the flora, which might later be replaced by a flora of the oceanic island type.

There are, however, to be found in oceanic islands some plants of which

we must at present remain in doubt as to the way they reached there. Such plants as *Panicum Andrewsii* and *P. clivale*, *Procris pedunculata*, *Asystasia alba*, *Datura alba*, *Hibiscus Vrieseanus* of Christmas Island, the *Cuscutas* and *Paspalums* of Fernando de Noronha, are very difficult to account for; most of them are endemic. The seeds, which are in most of them small, may have been imported on crevices of logs, or in pumice, or possibly swallowed with grit by birds, and later thrown up, but the ordinary methods of dispersal—sea, wind, or swallowing by or adhesion to birds—will not entirely account for their presence there.

That some at least of the flora may be brought by sea-drifted logs to oceanic islands is tolerably certain. In former times it was thought that the presence of terrestrial molluscs on an island was a proof that it had been formerly land-connected, but the recent discovery of snails in Krakatau shows that they can cross the sea, doubtless in drift-timber, readily and abundantly. The presence of abundance of ants, reptiles, shrews and rats (as in Christmas Island) corroborates this. It is impossible to see how otherwise they can cross the sea.

The greater part of an oceanic island flora, however, is derived from seeds drifted by sea, dust-seed more rarely, plumed seed or fruits, and spores brought by wind, and seeds or fruits adhesive to birds, or those of drupes or berries swallowed by birds or bats, and later evacuated.

Unfortunately, in the case of remote islands, nearly all have been visited and settled on by man before the botanists arrived to investigate the flora, and even when the first botanists did arrive at an island, only very small collections were made. Mere casual landings of whalers and sealers seem in but few cases to have been responsible for plant introductions, though we have known of a few plants (mentioned elsewhere) so brought, nor have shipwrecks made any known instances of additions to floras.

Endemic plants serve to throw the greatest amount of light on the flora of an island, as it may be taken for certain that these cannot have been introduced by man.

There are a few islands, however, in which the flora has been investigated by naturalists before the settlement of any human beings there. Among these the most important are Christmas Island, South Trinidad and Martin Vaz, and the Island of Krakatau. Of this latter island, lying 25 miles south of Java, the whole flora was completely destroyed by an eruption of the volcano in August 1883, so that it and the adjacent islands, Lang and Verlaten, were covered with a layer of pumice and ash to a depth of from 98 to 196 feet deep, and where the least amount fell, red-hot stones completed the destruction of the fauna and flora of this formerly heavily-forested region. The Dutch botanists visited the islands in 1886, 1897, 1906 and 1919, and made records of plants they found on each occasion. Except that in 1917 an European with many coolies settled for some time in the north-east corner of Krakatau, no human beings visited the island, apart from the expeditions. According to Lotsy, an old *Cycas* found by Valeton was a survivor of the eruption. I think it just possible that a few of the hard seeds of the *Leguminosae*, such as those of *Albizzia stipulata* and *Cassia siamea*, which appeared later, may have survived the destruction, buried in ash, and were afterwards exposed by denudation, and grew. They seem to have no means of dispersion by wind, water, or birds adequate to account for their presence.

Cocos-Keeling Island is a small coral atoll 700 miles from Java. The first botanical collections from there were made by Charles Darwin in the voyage of the "Beagle," 1836, 9 years after the first settler (Hare) had settled there. The plants he found there were:—Sea-dispersed: *Hibiscus tiliaceus*, *Triumfetta procumbens*, *Acacia Farnesiana*, *Guilandina bonduc*, *Pemphis*, *Portulaca oleracea*, *Guettarda*, *Ochrosia parviflora*, *Scaevola*, *Cordia subcordata*, *Tournefortia argentea*,

Stenotaphrum lepturoide, *Lepturus repens*; and A. S. Keating, who also visited it early, records Coco-nut and *Aleurites moluccanus*, probably sea-borne. Adhesive plants were: *Dicliptera Burmanni*, *Boerhaavia diffusa*, *Pisonia excelsa*, *Achyranthes argentea* and *Urera Gaudichaudiana*. *Digitaria sanguinalis*, which was there, may have been borne adhesively by a sea-bird or accidentally brought by Hare. Keating mentions the drifting of Sago Palm trunks and timber to the atoll, and Bali coco-nuts, seed of *Erythrina*, *Sapindus saponaria*, and Castor-oil beans. Ross told me of the drifting of living and growing Sugar-cane there. A number of other plants have since been introduced accidentally by man and by natural causes. Some were collected by Forbes in 1879, and some later by Robinson in 1911. The most interesting additions were, Sea-borne: *Morinda citrifolia* (1879), *Terminalia catappa* (1911), possibly both introduced by man, *Ipomoea denticulata*, *Fimbristylis cymosa* and *F. spathacea* and *Mariscus albescens* (1911). *Stachytarpheta indica* (1879), *Sonchus oleraceus* (1879), *Vernonia cinerea* (1911), *Sida carpinifolia* (1879), *Abutilon indicum* (1911), all brought by man.

Considering the number of seeds which must be drifted to the island, the number of native plants is very small, doubtless from the soil being almost all coral. Ducks, the Philippine rail, weaver-birds, sea-birds, reef-herons, and fox-bats have from time to time reached the island.

Christmas Island lies 194 miles south of Java, and is an ocean island of 3 elevated coral reefs on a core of basalt, with a few shingle beaches, but no sand. It was first visited by Capt. Maclear in the "Flying Fish," 1886—he collected a few plants—then by J. J. Lister in the "Egeria," 1887. Till then the island had been uninhabited. In 1888 G. Clunies Ross settled there, and some introduced plants appeared. I visited it in 1890, and collected what I could in 10 hours. In 1897 C. Andrews spent a year there, and collected largely. By this time the island was being worked for the phosphate, and one goat had been introduced. In 1904 I visited it again for a month, and collected plants widely. By this time ponies and some cattle had been imported, but the weeds introduced were confined to the Settlement, and the greater part of the island was in its natural state. There are 42 sea-dispersed plants, and 5 or 6 kinds of commonly sea-borne plants have drifted to the coast, though they failed to establish themselves. Wind-borne are: 1 *Composite*, *Blumea* and a *Hoya*, 10 *Orchids*, 1 *Balanophora*, 24 *Ferns*, 2 *Lycopodiaceae*, 15 mosses and 3 Hepatics, and some fungi. Bird-borne plants, drupaceous and baccate, about 32, and 17 adhesive.

Of these plants, almost all are Javanese or have Javanese affinities, but *Cryptocarya* (bird-dispersed), *Ischaemum nativitatis* (possibly adhesive to birds), *Inocarpus edulis* and *Fimbristylis cymosa* (sea-dispersed) are of Australian affinity or origin. There are a fruit-bat, 4 frugivorous birds, a rail, a cuckoo, 2 wag-tails, a heron, 8 waders and a duck, which constantly reside in or visit the island.

Contrast Between the Floras of Krakatau, Christmas and Cocos-Keeling Islands.

I take the first two of these islands for comparison, because they are two of the best samples we have of islands whose flora is known before they have been interfered with by man. I add Cocos-Keeling, which is at a greater distance from Java than the other two, and which consists of coral reef only, so as to compare it with the other two. There are several differences in the environments of the flora in these islands which have a marked influence on the plants found in them.

(1) *The temperature* (tropical) is approximately the same in all three. The

nearest land to the islands is Java, and the first difference to be noted is the distance—Krakatau, 25 miles, Christmas Isle 140 miles, Cocos-Keeling 700 miles.

(2) *The soils.*—In Krakatau the island is composed of volcanic ash and mud, suitable for most plants of the tropics; in Christmas Island, mainly 3 large coral reefs based on basalt, which (chiefly in the lower part of the island) comes to the surface in various spots, so that the soil, guano and coral, is strongly impregnated with lime, and only suitable for calciphilous plants; Cocos-Keeling, a coral atoll, entirely lime, with a little sand from the sea-bottom thrown up here and there.

(3) *Rainfall.*—The rainfall in Krakatau amounts to 98 inches a year, chiefly December and March, and there is comparatively little rain between the months of May and September, the dry season. Ernst records the occurrence of broad streams.

Christmas Island has a heavy rainfall from December to May, the rainy season, after which it becomes very dry. Owing to the calcareous reefs which form the bulk of the island being very permeable to water, the only permanent streams are found where the coral overlies the basalt, and some plants could grow only where this water lay. Naturally there were hardly any streams or stagnant water. Cocos-Keeling.—We know practically nothing of the rainfall, but it has no streams or marsh land.

(4) *Winds.*—In Krakatau, apparently, the wind blows steadily from the east or south-east, but during the rain monsoon the wind blows from the north-west. In Christmas Island the prevalent wind is south-east or east south-east for part of the year, but from December to May the wind is north or north-east, and then, as Andrews states, is the time of the arrival of wagtails, whimbrels, swallows and other birds, as well as butterflies and dragon-flies. In Cocos-Keeling Ross reports that the wind is chiefly south-east or east south-east, and rarely north-east. It is also liable to typhoons every few years, which might destroy the larger trees.

(5) *Sea Currents.*—There are certainly currents from Java to Krakatau, and from Krakatau to Christmas Island, as I found much pumice from that island on the shores of Christmas Island, but from the occurrence there of some of the sea-borne plants of further east, I conclude that there is also a current running from east to west. There is evidence of a strong current running to Cocos Island from Papua and the Moluccas (Keating).

The flora of Krakatau (to the last record of collections in 1919) is only 36 years old; Christmas Island, as an island above water, dates from the Eocene period; Cocos Island is of unknown date.

Krakatau has many more wind-borne plants than Christmas Island, as it contained plumed grasses and *Compositae*, which could be carried the shorter distance. Its greatest number of vascular cryptogams is probably due to more suitable soil.

Bird-dispersed plants—34 Krakatau, 36 Christmas Island—are about equal. Adhesive fruits are more numerous in Christmas Island, perhaps due to the much larger number of sea-birds there formerly. Plants with seeds possibly brought in mud, on birds' feet, are few in Krakatau, and fewer (or none) in Christmas Island in spite of the visits of waders, as there is no suitable ground for them. Sea-borne plants are rather more numerous in Krakatau than in Christmas Island, but that is undoubtedly due to the absence of sandy beaches in the latter, as it is the sand plants which are missing.

Cocos-Keeling, a smaller group and entirely of coral reef, has many fewer plants, 17 sea-borne and 5 adhesive plants being all that appear to be indigenous, yet we know that strong currents bring much sea-drift to the islands. The absence of plants with drupes or berries is doubtless due to its long distance

from Java. The adhesive ones are doubtless brought by sea-birds and herons. The abundance proportionately of these plants in the two islands most haunted by sea-birds shows to what an extent these birds carry adhesive fruits.

FLOWERING PLANTS.

	Sea-borne.	Wind.	Berry or Drupe.	Ad-hesive.	Mud on Birds.	Doubtful.	Total.	Vascular Cryptogams.	
								Pteri-dophyta.	Bryo-phyta.
Krakatau .	60	34	34	9	3	4	144	48	19
Christmas .	44	9	36	15	0	7	129	25	18
Cocos-Keeling	17	0	0	5	0	—	22	0	1

The contrast between the floras of the three islands is clearly shown by the table. I have excluded cellular cryptogams because they have been so irregularly collected and studied.

The plants I record as of dubious method of transport in Krakatau are *Stemona parviflora*, *Radermachera glandulosa*, *Aristolochia Tagala* and *Dioscorea* sp., all plants with winged seeds, which seem to me hardly likely, however, to be blown across by wind; possibly they were sea-drifted. The *Dioscorea* may be *D. bulbifera*, of which the bulbil tubers float. The only parallel I know to winged seeds reaching oceanic islands, unless modified for sea-dispersal as well, is the occurrence of *Tecoma roseoalba* in Fernando de Noronha, of which, however, the fruit is not known, though it is probably winged. There are hardly any plants of human introduction in Krakatau. *Eleutheranthera ruderalis* was undoubtedly brought by accident in some of the baggage from Buitenzorg, almost the only spot in the Old World where it occurs, and probably *Synedrella nodiflora*, *Eclipta alba*, and *Eleusine indica*, came in the same way. The other two islands have, of course, numerous plants of human introduction.

VOLCANO ISLAND.

This is an island in the middle of Lake Bombon, in the Philippines, in which an eruption of mud, accompanied by steam and sulphur dioxide smoke, destroyed the inhabitants and almost all the plants in 1911. The flora was investigated in 1917, and an account published by W. H. Brown, E. D. Merrill, and H. S. Yates (in the *Phil. Journ. Sci.*, xii, 177, 1917). The island is not far off the mainland, and some trees survived at one end of the island, as did apparently plants of *Musa*, Bamboos, and rhizomes of *Saccharum spontaneum*, though deeply covered with mud. In 1916 no less than 292 plants were recorded from the island: of these, 82 had drupes or berries, and 14 had adhesive fruits; 60 species had minute seeds which might have been conveyed in mud on birds' feet, 60 species were wind-borne—of these, there were 19 Ferns, 1 *Lycopodium*, 1 *Selaginella* and 2 Orchids—39 species eaten and passed by cattle, and 21 of human introduction, for by 1916 natives had again settled there. *Ottelia alismoides*, *Vallisneria gigantea*, *Pistia stratiotes*, *Lemna trisulca* and *L. polyrrhiza* and *Ceratophyllum demersum* had drifted to the shores. In the sea-drift were seeds of *Inga Saman*, *Citrullus vulgaris*, and *Cucurbita maxima*, and a sound fruit with seeds of *Artocarpus integrifolia*.

Compared with the re-afforesting of Krakatau, we notice that the destruction by volcanic action was not so complete, and that the island was considerably nearer the mainland and not isolated by sea-water. A very large number of terrestrial (i.e., not sea-dispersed) *Leguminosae* occur in the list. We know that the seed of these plants can remain buried for many years and be germinable, and one can hardly doubt that the plants are derived from seeds buried unharmed in the mud, and it is quite possible that those of many other species formerly on the island escape destruction in a similar manner. This, and the propinquity of the land, account largely for the extensive flora. The large number of bird-dispersed plants is interesting, as showing the very important part played by them in reclothing land with vegetation.

Notes on the Various Islands.

Canary Islands lie 50 miles only from the coast of Africa (Cape Juby). Many geologists claim here a land bridge across the Atlantic connecting both sides, America and Africa, and including the Canary Islands. The littoral molluscs are said to be the same on both sides. Scharff says that Madeira and the Azores were connected with Portugal, and a broad stretch of land lay from Morocco to the Canaries and to South America, and as far south as St. Helena. Arldt gives a peninsula from southern Morocco to the Canaries and Cape Verde. Wallace, Christ, Vahl, Schimper and Engler seem to consider there has been no connection between these islands and any mainland. Pitard ("Iles Canaries") gives, however, evidence of a land connection with South America in the occurrence of *Drusa* (*Umbelliferae*), *Bystropogon* and *Cedronella* (*Labiatae*), of which American genera endemic species occur in the Canaries. *Waltheria elliptica* and *Ipomoea littoralis* are also American types which may have come by sea or in ballast. I see little connection with the flora of St. Helena.

From a point of view based on the dispersal of seeds and the usual type of oceanic islands, we have to notice that the number of indigenous species in the Canaries is remarkably large, and the number of endemic species in a genus is unusually large. Thus though in an oceanic island never connected with the mainland it is rare to find more that 3 or 4 species in a genus, we have in the Canaries 16 endemic species of *Senecio*, 9 of *Lotus*, 17 of *Sonchus*, 20 of *Micromeria*, 13 of *Statice*, 18 of *Echium*, 10 of *Euphorbia*, 32 of *Aeonium*, an endemic genus. Again, the flora includes numerous plants incapable of crossing the sea, notably the endemic *Pinus canariensis* and *Quercus lusitanica* var. This evidence should be enough to establish the fact that the Canaries are not oceanic islands, and that the flora of the present day is derived from the western corner of the Mediterranean region and the West Coast of Africa by a land connection.

Madeira is 450 miles from Morocco. There is every reason to believe that it is, like the Canaries, a continental island formerly attached to North Africa. The flora is a large one, and contains many endemic, or, probably more correctly, epibiotic species. Sea-dispersed plants are represented by *Cakile* and *Crithmum*, *Calystegia*, *Soldanella*. Wind-dispersed: many plumed *Compositae*, *Salix*, 4 Orchids, and 46 vascular cryptogams. Drupaceous and baccate fruits, readily bird-dispersed, are most of the trees: *Pittosporum*, *Ilex*, *Ardisia*, *Sideroxylon*, *Notelaea*, *Persea*, *Ocotea*, *Laurus*, *Myrica Faya*, *Sambucus*, *Berberis*. The flora is, on the whole, allied to that of the Canary Islands and Morocco.

Cape Verde, 50 miles from Senegal, is also probably a continental island group. Sea-borne plants are: *Ipomoea biloba*, *Guilandina bonduc*. Wind transport: many plumed *Compositae*, *Statice*, *Sarcostemma*, 1 Orchid, and 15 vascular cryptogams. Drupaceous and berried plants: *Asparagus*, *Cremaspora*, *Pavetta*, *Canthium*, *Vitis* (3 or 4), *Loranthus*, all of African affinities.

Adhesive: *Boerhaavia*, *Triumfetta*, *Forskahlea*, *Aerua javanica*. And probably attached in mud to birds' feet; *Cladium mariscus*, *Fuirena*, *Mariscus umbellatus*, *Potamogeton*, *Frankenia*.

The whole flora is practically of African origin, and bears little relation to that of Madeira and the Canaries. All these islands contain a great number of plants of human introduction, having been long settled in by man.

Azores, a group of islands lying 900 miles from Portugal and 550 from Madeira, discovered in 1432, and long inhabited. Since their discovery a large number of plants have been intentionally or accidentally introduced by man. When discovered, they were densely covered by a forest of trees, almost exclusively introduced by birds, a large proportion of which trees have been destroyed by volcanic action and by the residents. The greater number of the species in the islands are European or of European affinities, a considerable proportion occurring in Madeira. Two plants, *Cakile* and *Solidago*, are American. All the indigenous trees and shrubs are bird-dispersed: *Ilex Perado*, *Rhamnus latifolius*, *Prunus lusitanica*, *Rubus*, *Hedera canariensis*, *Viburnum Tinus*, *Vaccinium cylindricum*, *Notelaea excelsa*, *Corema album*, *Myrsine africana*, *Daphne laureola*, *Laurus canariensis*, *Persea indica*, *Smilax canariensis*, *Myrica Faya*, *Juniperus brevifolia*, *Taxus baccata*, *Ruscus aculeatus*, *Arum italicum* and *Iris foetidissima*. About 8 frugivorous birds visit the island.

Adhesive fruits, doubtless bird-borne, are: *Sanicula azorica* and *Arceuthobium oxycedri*, and I should suggest also the following grasses—*Deyeuxia* (2 endemic), *Festuca* (2, 1 endemic), *Holcus rigidus*, *Gaudinia geminiflora* (both endemic), possibly the North American *Solidago sempervirens* also. Sea-borne plants are: *Cakile edentula*, of North America, *Crithmum maritimum* and *Polygonum maritimum*, *Euphorbia peplis* and *E. azorica*, and *Juncus acutus*; *Salsola Kali* and *Beta maritima* probably were imported in ballast, as Guppy suggests the *Cakile* was. Wind-dispersed are the orchids *Serapias cordigera*, *Habenaria micrantha*, and *H. longibracteata*, with 30 ferns and 4 *Lycopodiaceae*, possibly also some of the endemic plumed *Compositae*, *Senecio*, *Tolpis* and *Microderis*. There are, besides, a large number of small-seeded plants whose presence is somewhat difficult to account for, but some of which were doubtless brought by waders and other birds in mud attached to their feet, beaks, or feathers. The following species were almost certainly so borne, as we know they have been transported in this way elsewhere, as explained under that section (*see* p. 549): *Hydrocotyle vulgaris*, *Sibthorpia europaea*, *Elatine hexandra*, *Anagallis tenella*, *Callitriche verna*, *Peplis portula*, *Littorella lacustris*, *Luzula* (*L. purpureo-splendens*, endemic), *Tillaea muscosa*, *Cladium mariscus*, *Heleocharis palustris*, *H. multicaulis*, *Scirpus fluitans*, *S. savii*, *S. setaceus*, *Carex* (several species), *Isoetes*, probably also *Frankenia* (2 species), *Illecebrum verticillatum*, *Galium palustre* and *G. anglicum*, *Polycarpon tetraphyllum*, *Lysimachia nemorum*, *Spergularia marina*, *Myriophyllum alterniflorum*, *Helosciadium nodiflorum*, *Ceratophyllum demersum*, *Alisma plantago*, *Lemna minor*, *Samolus valerandi* and some *Potamogetons*.

More difficult to account for are *Calluna*, *Erica*, *Thymus*, *Polygala*, *Potentilla*, *Seubertia azorica*, *Campanula Vidalii* (compare the wide distribution of *Wahlenbergia* in the Antarctic area, Juan Fernandez, etc.), *Erythrea Massoni*, *Veronica Dabneyi*, *Euphrasia grandiflora*, *Myosotis* (2 species), *Nasturtium*, *Cardamine*, *Cerastium* and *Vicia*. Most of these species are endemic.

It is, however, possible that these plants were brought in mud on birds' feet, as a considerable number of waders, rails, herons and ducks constantly visit the islands.

No genus of plants contains more than 4 species, except a few introduced ones, which suggests that the islands have never been connected with the mainland.

Atlantic Islands.—Ascension Island lies 698 miles north-west of St. Helena. It was discovered about 1502. A volcanic island, apparently never connected with any other large extent of land, its indigenous flora is very poor. The first collector, Cunningham (1698), obtained only 5 plants, the small *Euphorbia origanoides* (endemic), *Aristida ascensionis* (possibly originally introduced by man), a *Hibiscus* (perhaps *H. trionum*, but the specimen has been lost, and the plant has not been seen again), and *Ipomoea biloba*, long since disappeared. Since then there have been discovered an endemic *Hedyotis* and *Rubus nanus*, recently discovered, and which it is suggested is only a form of some escaped species. A scrap of a plant brought by Lesson in 1829 appears to be an *Ouratea* (*Gomphia*) of American affinity. It has not been seen since. A species of *Juncus* is certainly indigenous, as possibly are *Mariscus umbellatus* and *Cyperus Haspan*; *Portulaca oleracea* is probably a human introduction; *Polypogon ascensionis* is perhaps a variety of *P. monspeliensis*, and it and *P. strictus* and *Sporobolus durus* may have been introduced by adhering to the feet or feathers of the numerous sea-fowl.

As in St. Helena, sea-borne plants are scarce, the *Ipomoea* being practically the only one. The doubtful *Ouratea* and *Rubus* may have been brought by a frugivorous bird. The rest seem to have been brought attached to the bodies of sea-fowl. There are also 15 Ferns, 2 *Lycopodiums* and *Psilotum*.

St. Helena.—This island is 1,140 miles from South Africa and 698 miles from Ascension. It does not appear to have ever been connected with any large body of land. It has long been colonised, and a large number of the plants recorded by Melliss and by Hemsley, in the "Voyage of the Challenger," are introduced plants. There is, however, a large endemic flora, and from these plants we can gather how the island obtained its vegetation. Sea-borne plants are scarce. *Ipomoea biloba* occurs, and seeds of *Entada* sp. and *Guilandina bonduc* have been drifted ashore, and perhaps the one or two endemic species of *Sium* may be sea-borne, as the mericarps are corky. It is clear that the coast is unsuitable for the sea-dispersed plants; neither *Entada* nor *Guilandina* have established themselves. Wind-dispersed plants are 7 endemic tree Composites, *Commidendron* and *Senecio*, and there are 25 species of ferns and 2 Lycopods. The scarcity of berries and drupes is obviously due to the fact that no frugivorous birds are known to occur, or to have occurred, on the island, and in this it contrasts with Tristan d'Acunha with its thrush. Some bird may have transported *Lobelia scaevifolia*, the only fleshy-fruited plant on the island.

Adhesive plants are *Petrobium* (*Compositae*), with bristly achenes armed with 2 acute sepaline points, 2 species of *Cotula*, with viscid achenes, and *Boerhaavia verticillata*, all of which might have been brought by sea-birds.

Seeds and Fruits carried in mud.—It is in small-fruited and small-seeded fruits, such as might be introduced by birds carrying the seeds in mud, that St. Helena is richest: *Frankenia*, *Mesembryanthemum*, *Melhania* (2 species), *Pelargonium*, *Hedyotis*, *Tripteris* (a composite with a small smooth achene), *Plantago*, *Mellissia*, *Acalypha*, *Senebiera*, *Heliotropium*, *Carex* (2), *Fimbristylis*, *Agrostis*, *Eragrostis*, *Desmaziera* (all endemic), and *Suaeda fruticosa*, *Juncus lomatophyllus*, *Cyperus laevigatus*, *Scirpus nodosus*, *Euphorbia Chamaesyce*, more widely-distributed plants. The affinity of the indigenous plants is with South Africa, the nearest land except Ascension, though very far distant (1,140 miles). It is probable that these plants were all introduced by sea-birds from the coast of Africa, but some possibly from the southern Antarctic regions.

South Trinidad and Martin Vaz.—These islands are 600 miles from Brazil, and seem never to have been attached to the mainland. No settlements have ever been made there, though whalers have occasionally touched them. The flora is not thoroughly known, as the islands are very difficult to land on

or to explore. South Trinidad was formerly covered with large trees, now perished; from wood specimens they appear to have been an *Eugenia*. The present flora is very scanty. Sea-transported plants are: *Canavalia* sp., *Alternanthera paronychioides*, *Ricinus communis* and *Cyperus atlanticus*. The *Alternanthera* is a seashore creeping plant with very small achenes, common in South America and the West Indies; a species occurs in Galapagos. The *Eugenia* was doubtless bird-borne. Wind-borne are probably *Achyrocline disjuncta*, a plume-fruited composite, an Orchid (genus unknown), found by Meade-Waldo in the Earl of Crawford's expedition, and 4 Ferns. A species of *Abatia* (*Samydaceae*), with capsules of minute seeds, *Fimbristylis nesiotis* (endemic), and *Sporobolus virginicus*, might have been brought attached to birds in mud, or on drift timber. Sea-birds are abundant, but no land-birds have been seen there.

Fernando de Noronha is a small group of islands about 5 miles long, consisting of 1 large island 4 miles long and 1 mile wide, with some smaller islands. It is entirely volcanic, and appears never to have been attached to the mainland. The group lies 200 miles off the north-east Brazilian coast. It is xerophytic in nature, hence the great scarcity of vascular and cellular cryptogams. It was discovered by Vespucci in 1504, and was for many years a convict settlement for Brazil, and thickly populated. Formerly densely forested, much of the arboreal vegetation was destroyed for cultivation, and to prevent the convicts making boats in order to escape. Many plants were introduced from the mainland. The first collections were made by Darwin ("Voyage of the 'Beagle'"), and by the Challenger Expedition, but the first extensive collections were made by myself, the Rev. T. S. Lea, and G. Ramage, who spent nearly a month on the island in 1887.

Taking only the endemic plants, and some which were unlikely to be introduced by the colonists, we found of sea-borne plants 21 species; wind-dispersed, 1 *Gonolobus* with plumed seed (*Asclepiadaceae*), 1 Fern, and a few mosses, 1 wing-seeded plant, a *Tecoma*, may possibly have been floated over by sea. The absence of the plume-seeded *Bromeliaceae* and of orchids, so common on the mainland, is rather remarkable, but the latter are rather dependent on a good supply of rainfall and permanent air-moisture. The birds on the island were a Dove (*Zenaida*), a Tyrant (*Elainea*) and a *Vireo*, and a number of *Charadridae* visited the island also, and there were many sea-birds. Plants with drupes or berries were 26, with fruits adhesive to feathers 14, and those liable to attachment to birds' feet in mud 16. Among the latter was a *Nitella*, which, accompanied by *Paspalum brizoides*, was abundant in a lake in the centre of the island, seldom visited by the residents. Some others of the small-fruited and seeded plants of wide distribution may also have been introduced by natural means, but it is impossible to say now.

The whole flora is evidently derived from the adjacent coasts of Brazil.

Bermudas, 580 miles from North Carolina.—Of the plants considered as indigenous, we find 32 are sea-dispersed, those with drupes or berries suitable for bird-dispersal 16, adhesive 12, wind-dispersed 10, and vascular cryptogams 24. There are 2 species of *Lemna*, probably brought by adhesion to water-fowl, and 31 small-seeded marsh or shore plants, probably brought by adherence to the feet of birds.

Hemsley suggests that *Sida carpinifolia* is indigenous, but, as I elsewhere remark, the way that this common seashore plant gets diffused is quite obscure, and I think it is generally introduced by man. *Desmanthus virgatus* and *Leucaena glauca* seem to me also as dubiously native. The latter is now widely distributed all over the world, and is certainly carried about by man. *Statice Lefroyi*, an endemic plant, must, I suppose, have been sea-dispersed, the winged fruit is not hairy, and it could hardly have been brought by wind. *Euphorbia*

buxifolia may be sea-floated, and the 2 endemic *Borrichias* (*Compositae*), the achenes not plumed but smooth and almost hairless, are difficult to account for unless by sea-transport. *Pilea microphylla*, *Sisyrinchium bermudiamum*, *Carex bermudiana*, and perhaps *Stenotaphrum americanum*, doubtless have arrived in mud on birds' feet.

Antarctic Islands. Tristan d'Acunha.—This island is 5,520 miles from Montevideo and 1,760 miles from South Africa. The flora is typically Antarctic, but is rather a curious mixture, with traces of African flora. It has no connection with St. Helena. The flora consists of 2 sea-dispersed plants, *Apium australe* and *Calystegia Soldanella*, several bird-dispersed plants with berries, *Phylica*, *Nertera* (2 species) and *Empetrum*. Unlike most of the Atlantic islands, there are land-birds, a thrush and a rail. Adhesive-fruited plants, doubtless brought by sea-fowl from the south, are *Uncinia*, *Acaena*, and probably *Spartina arundinacea*. Viscid-fruited fruits are 2 species of *Cotula* and, perhaps, *Chenopodium tomentosum*. Wind-borne plants are *Chevreulia stolonifera*, a South American Composite, 2 species of *Gnaphalium*, 24 Ferns and 2 *Lycopodiums*.

The remainder of the indigenous plants are mostly small-seeded, and are, perhaps, transported as seed or fruit in mud on birds' feet or feathers. They are mostly of Antarctic affinities, and consist of species of *Ranunculus*, *Cardamine*, *Polycarpon* (perhaps introduced by man), *Hydrocotyle*, *Carex* (2 endemic), *Agrostis* (one with awned and the other with un-awned spikelets), *Rumex fruticosus* (endemic, with rather large-winged fruit, possibly sea-borne), and *Pelargonium*, allied to South African species.

Gough Island is 280 miles from Nightingale Island, Tristan d'Acunha, 1,500 miles from the Cape, and 2,000 miles from Cape Horn. Its flora resembles that of Tristan d'Acunha. Bird-dispersed: *Phylica* (2), *Empetrum* (adhesive), *Cotula* (endemic), and the *Chenopodium* and *Spartina*, and 2 *Agrostis*. Sea-borne: *Sophora tetraptera* and *Apium goughense*, allied to *A. australe*. Wind-dispersed: 1 *Gnaphalium*, 10 Ferns, 2 *Lycopodiums*. The birds are 2 species of *Neospiza*, 1 *Thalassogeron*, a rail, and sea-birds.

The Kerguelen Group.—This scattered group of islands comprises Marion Isle, the Crozets, Prince Edward Isle, Kerguelen, and Heard Island. Marion Island is about 960 miles from South Africa, 1,200 miles from Kerguelen, 2,150 miles from Tristan d'Acunha, and 4,510 miles from the Falklands and Fuegia.

The flora is apparently entirely Antarctic. Darwin suggests that Kerguelen had been stocked by seeds brought on icebergs. Hooker suggested that these islands are the remains of a lost land, being the peaks of a range of mountains running east and west, and part of this lost land included what are now Amsterdam and St. Paul's Islands. This theory was, to some extent at least, confirmed by the Challenger Expedition.

There are no frugivorous birds on these islands, so that plants with drupes or berries are not represented. There are, however, many sea-birds and a local teal.

The plants represented are:—*Ranunculus*, *Colobanthus* (*Cruciferae*), *Montia fontana*, *Tillaea moschata*, *Azorella* (*Umbelliferae*), *Galium*, *Limosella aquatica*, *Callitriche*, *Juncus*, *Deschampsia*, *Agrostis*, *Poa*, *Festuca*, *Nitella* (all of which might be carried by birds in mud attached to feet or feathers), *Cotula* (viscid), *Acaena* and *Uncinia* (armed, and readily attached). Wind-dispersed: Ferns 4, Lycopodiaceae 2. To these are added the two most characteristic Kerguelen plants, *Pringlea antiscorbutica* and *Lyallia*.

Pringlea antiscorbutica, the Kerguelen cabbage, is confined to Kerguelen, Heard, and Marion Islands. The seeds are the main food of the local teal. They are too soft and perishable to pass unharmed through the bird, and are

not likely to be transported on their feet or feathers. The presence of a wingless fly in both Kerguelen and Heard seems to show that the islands were formerly connected, which is also confirmed by the occurrence of freshwater fish identical with species occurring in New Zealand, Tasmania, and the Falklands and South America. These facts, with the occurrence of fossil tree trunks in Kerguelen, are confirmatory of the theory of a large extent of land, and a larger flora here.

South Georgia.—A small island in the Antarctic regions, about 900 miles from the Falkland Islands. It has been visited by one or two expeditions, and Skottsberg ("Geographical Distribution of Vegetation in South Georgia," *Geograph. Journ.*, Nov., 1902) gives the latest account of it.

The flora consisted of *Ranunculus biternatus*, *Colobanthus subulatus* and *C. crassifolius*, *Montia fontana*, *Callitriche verna*, *Galium antarcticum*, *Acaena ascendens*, *A. laevigata*, *Juncus Novae Zealandiae*, *Rostkovia magellanica*, *Poa flabellata* (*P. caespitosa*), *Phleum alpinum*, *Festuca erecta*, *Aira antarctica*, all doubtless brought attached to the feathers or feet of the sea-birds; 3 Ferns, a Lycopodium, 52 Mosses, 11 Hepatics, doubtless brought by wind. *Poa pratensis* has been brought accidentally by whaling-boats and established itself near the stations. Most of the flora occurs also in the Kerguelen Group; a few are obviously derived from Fuegia, and the *Juncus* from New Zealand.

New Zealand Group. Chatham Islands, 360 miles from New Zealand. The flora has been described by J. Buchanan (in *Trans. New Zealand*, vii, 1875, 333). It contains Bird-dispersed plants (18 species), Adhesive (4), Viscid fruits, 3 *Cotula*. Wind-borne: Epilobium (6), Plumed Composites (13), Orchids (10), Ferns (40), *Lycopodium* (7), *Potamogeton natans*, *Triglochin*, *Ruppia*, *Drosera*, *Haloragis*, *Callitriche*, *Myriophyllum*, and some others perhaps borne on feathers of birds, as may also be 7 awned grasses, a *Festuca* and *Poa*. Besides these, however, there are a number of plants distinctly not insular: *Viola*, *Geranium*, 3 genera of *Ericaceae*, *Gentiana*, *Libertia* and *Phormium*. The whole flora suggests these are continental islands formerly attached to New Zealand.

Auckland Isles and Campbell Island lie about 180 miles from New Zealand. Their floras are very similar. Bird-dispersed (12), (*Coprosma* 6). Wind-dispersed: *Helichrysum* and *Celmisia*, with plumed achenes, *Epilobium* (3), Orchids (7), Ferns (15), Lycopods (3). Adhesive fruits, *Leptinella* (*Compositae*), *Uncinia* and *Acaena*, and possibly *Pleurophyllum* (2 species), with spiny achenes, and *Urtica*, *Ranunculus* (2) style hooked; awned grasses, *Hierochloa*, *Bromus*, *Trisetum*. Sea-dispersed may be *Aciphylla*, an Umbellifer with large corky fruit. There are also a very considerable number of small-seeded plants like *Tillaea*, *Montia*, *Plantago*, *Juncaceae*, *Cyperaceae*, which we know to be transported in mud on birds' feet. But there are also a few plants like *Chrysobactron* (*Liliaceae*) and *Metrosideros*, which seem hardly likely to be so transported, and the whole flora suggests that the islands were formerly attached to New Zealand, most of the plants belonging to that island or allied, though a few, like *Rostkovia*, are Fuegian.

Norfolk Island is 400 miles from New Zealand. The flora is an Australian type, and the presence of an *Araucaria* and a *Tecoma* (*Bignoniaceae*) seems to show it is a continental island. It has 22 sea-borne plants. Wind-borne: *Tylophora*, *Gnaphalium*, *Clematis*, *Typha*, 7 Orchids, 40 Ferns and 3 Lycopods. Bird-dispersed 40, and adhesive 18, as well as a number of small-seeded species which may have been brought on birds' feet and feathers: *Frankenia*, *Viola*, *Wahlenbergia*, *Erythraea*, Sedges and grasses.

Macquarie Islands are 600 miles from New Zealand. They contain 1 bird-dispersed fruit with red drupes (*Coprosma*). Adhesive plants (4), *Acaena* (2), *Cotula*, *Uncinia*. Wind-dispersed: *Epilobium* (2), Ferns (2), Lycopod (1). Probably brought by adhesion to birds' feathers: *Ranunculus*, *Carex*

and 7 Grasses. In mud attached to birds' feet: *Colobanthus* (2), *Montia*, *Callitriche*, *Tillaea*, *Azorella*, *Luzula*, *Juncus*; and a few plants of dubious transport, *Stellaria*, *Cardamine*, *Stilbocarpa*.

Islands of the Arabian Sea.—These are the Laccadives, Maldives, Minikoi and Chagos. All of them have been settled on by man for a considerable time, and numerous weeds have been introduced. The Laccadives are between 120 and 180 miles from the Indian coast, Maldives 300 miles from Cape Comorin and 400 miles from Ceylon, Minikoi and Chagos farther south, and about as near to the Seychelles as to the Maldives. All are coral islands to a large extent, and Diego Garcia (Chagos) is a simple coral atoll like Cocos-Keeling. Sea-dispersed plants form the largest element in the floras of all. The Maldives and Laccadives have about 54 species, Minikoi 30, and Chagos 22. Among these I class *Nothosaerua* and *Aerua lanata*, as Prain considers them to be sea-dispersed; but they might well be introduced in the down of sea-birds, as these fruits are certainly adhesive to the wool of sheep. Drupaceous and baccate fruits are not abundant, there are about 8 in the Maldives and 3 in Minikoi; in the Laccadives about 7, *Pleurostylia angulata*, *Vitis* (2 species), *Pavetta indica*, *Ficus retusa*, *Cephalandra indica* (but this possibly introduced by man), *Allophylus Cobbe* (a common seashore shrub with red drupes, may be introduced by sea, but more probably by birds; it is on all the islands). In Chagos, *Premna serratifolia* may be bird-dispersed, but more likely sea-dispersed. There are no other plants of this class there. Adhesive-fruited plants are represented by *Desmodium gangeticum* and *D. triflorum*, *Adenostemma viscosum*, *Anisomeles*, *Boerhaavia* (3 species), *Fleurya* and *Pouzolzia* in the Maldives, most of which occur in Minikoi also. In Chagos we have *Achyranthes aspera*, *Pisonia inermis*, and *Boerhaavia*. Small-seeded fruits, which might be introduced by birds in mud on their feet, are *Oldenlandia* (3 species), *Borreria ocymoides*, *Herpestes monniera*, *Rungia parviflora*, *Cladium mariscus*, *Pycreus pumilus* (Maldives), *Ammania baccifera* (a marsh plant), *Linaria ramosissima*, *Striga lutea*, *Polygonum barbatum*, *Aneilema ovalifolium*, *Cyperus hyalinus* (Laccadives) and *Chara* sp. (Laccadives).

Some of these may have been introduced by man, and *Herpestes* and *Striga* are closely associated with cattle. They also occur in Chagos, with other weeds of cultivation. Wind-dispersed plants are *Lactuca polycephala* and *Launaea* (*Compositae*), with plumed fruits, in the Maldives, and *Tylophora asthmatica* and *Leptadenia reticulata* in the Laccadives. Orchids are absent from all the islands.

Sporophytes are represented by 15 in the Maldives, 2 in the Laccadives, 2 in Minikoi, 6 in Chagos. These, however, depend more on suitability of climate than on the wind.

The Andamans and Nicobar Islands are undoubtedly continental, formerly connected with Burma and perhaps North Sumatra, as are also the Mascarene Islands, which retain a number of relics of a lost mainland, perhaps formerly attached to Africa, and Socotra, which is evidently a detached portion of Arabia, retaining also the remains of a more widely extended lost flora.

Polynesian Islands.—Of a large part of the vast number of islands and coral atolls in the Polynesian Archipelago, comparatively few have been completely investigated, and it is by no means certain that they are not remnants of a more closely-connected area. They have long been inhabited by a travelling sea-folk, who have certainly conveyed plants from one place to another, and it is clear that most of the cultivated plants, and probably many of the weeds, were derived from the Malayan region. In the islands nearest America a few plants from that country, sea- or bird-borne, have been met with in Hawaii and Easter Island. Sea-borne plants are naturally widely dispersed and abundant

on these islands, in which the coral beaches are suited for the growth of many species.

Easter Island lies 2,000 miles from South America and 1,400 miles from Pitcairn Island. It has long been colonised by man, and it seems that a large part of its flora has disappeared, and a considerable number of weeds of cultivation introduced. Skottsberg gives the latest account of its flora which contains sea-borne plants: *Ipomoea biloba*, *Apium prostratum*, *Guilandina bonduc*, *Calystegia sepium*, *Sophora Toromiro*, *Sesuvium portulacastrum*, *Thespesia populnea*, and probably *Cenchrus Hillebrandianus*. Wind-borne plants: 11 Ferns. Bird-dispersed: *Lycium sandwicense* (drupaceous). Seeds and fruits attached to birds' plumage or feet: *Boerhaavia*, *Triumfetta*, *Verbena littoralis*, *Polygonum*, *Samolus*, *Chenopodium ambiguum*, *Euphorbia serpens*, *Scirpus riparius* (*lacustris*), *Cyperus vegetus*, a Nasturtium, and a number of grasses. The flora is mainly Polynesian.

Pitcairn Island.—Maiden published an account, "Notes on the Vegetation of Pitcairn Island," based on a collection made on the island by a resident, but it is clear that this island, which lies between Easter Island and Tuamoto, but nearest to the latter group, has not been at all fully explored. It has long been inhabited, and a number of plants introduced. Of sea-borne plants, about 12 are recorded. Wind-dispersed are 4 Ferns, drupaceous and baccate plants about 8, the most interesting of which is *Osteomeles anthyllidifolia*. *Metrosideros villosa*, a widely-dispersed tree with capsules of small seeds, is difficult to account for; it also occurs in Macquarie Island. The flora seems Polynesian, and very different from that of Easter Island.

Rapa Island.—An account of this island, which is 250 miles south of the Austral Islands, is given by Riley (in *Kew Bull.*, 1926, p. 21). The island appears to have been long settled on, and cultivated by natives. The list of the flora given includes the following plants:—Wind-dispersed: *Fitchia nutans*, *Gnaphalium luteo-album*. Sea-borne: *Dodonaea viscosa*, *Hibiscus tiliaceus*. Bird-dispersed, baccate or drupaceous: *Cookia*, *Plectronia*, *Claoxylon* (all endemic species), *Dianella intermedium*, *Piper latifolium*, *Vaccinium cereum*. Adhesive to birds: *Peperomia leptostachya*, *Jussiaea suffruticosa* (in mud). Human agency: *Sida rhombifolia*, *Oxalis corniculata*, *Erigeron bonariensis*, *Verbena officinalis*, *Aleurites moluccanus*. Doubtful: *Phyllanthus* (an endemic species), *Weinmannia parviflora*.

Hawaii.—This group of islands is 700 miles from the nearest Polynesian islands, and 2,350 miles from America. It has a very rich flora, suggesting that it was formerly of much wider extent, and that it is of great antiquity. Some of the genera contain a considerable number of species, which is not at all usual in oceanic islands, and it includes a number of genera otherwise absent from such islands, such as *Viola* (5 species), *Silene* (4), *Labiatae*, *Hillebrandia* (*Begoniaceae*), winged fruits such as *Gouania*, *Mezoneuron*. Of sea-borne plants I find 40. Drupes and berries (195) (but the genera often contain numerous species). Wind-borne: Plume-fruited *Compositae* 27 (these are more likely to have been carried on the feathers of birds), Orchids 3, Ferns 128, *Lycopodiaceae* 10. The absence of any indigenous plume-seeded *Apocynaceae* and *Asclepiadaceae* is very marked. There are a considerable number of plants with adhesive fruits: *Tribulus*, *Sanicula*, *Daucus*, *Adenostemma*, *Boerhaavia*, *Pisonia*, *Achyranthes*, *Rumex*, *Peperomia* (10 species), *Uncinia*; and a large number which may have been brought in mud on birds' feet, *Drosera*, *Lythrum*, *Jussiaea*, *Hydrocotyle*, *Erythraea*, *Luzula*, *Naias*, *Ruppia*, *Scirpus lacustris* and *S. maritimus*, *Cladium*, *Rhynchospora* and *Marsilea*, and many others.

There is a distinct American element, and it is difficult to see how such plants as have American affinities could have crossed over 2,000 miles of sea.

Admiralty Isles are 130 miles from New Hanover, and as far from New Guinea. They were visited by Moseley in the Challenger Expedition, but the collections were much injured by decay, and are very incomplete. He obtained 33 sea-dispersed plants of the ordinary type, 41 drupes or berry plants dispersed by birds and bats, 7 plants with wind-dispersal mechanism, 31 Ferns, and 4 *Lycopodiaceae*, 3 species with hooked or spiny fruits, and 6 which might be conveyed by attachment to birds' feet. There were also species of *Lepidagathis* and *Hemigraphis* (*Acanthaceae*), and *Alchornea* (*Euphorbiaceae*), the means of dispersal of which are doubtful. In an Eastern tropical forested group of islands one would expect to find the largest proportion dispersed by the abundant birds and fox-bats.

Gilbert Isles, 100 miles from the Marshall Isles, 1,000 miles from Fiji and Samoa and Solomon Islands. C. M. Woodford collected all the plants he could find (*Geograph. Journ.*, 1895, p. 325). They include 13 sea-dispersed, 2 adhesive (*Boerhaavia* and *Tribulus*), 1 bird-dispersed (*Ficus*). The natives brought Coco-nut, Banana, Colocasia and Breadfruit, but apparently no weeds. Sea-birds, waders and the reef-heron haunt the islands.

Marshall Isles are a number of coral atolls. The flora is not well known, but E. Betche collected 12 sea-borne, 1 adhesive (*Triumfetta*), and a *Tabernaemontana*, probably bird-borne.

American Pacific Islands. Juan Fernandez and Masafuera.—These islands are 400 miles from the Chile coast, and the flora has naturally American affinities. They have been colonised for a long period, and contain many introduced plants. Only 3 plants can be classed as sea-borne. Of fruits swallowed by birds and dispersed, I reckon 36, including a Bromeliad, *Ochagavia*. Of adhesive-fruited plants there are 10, mostly grasses; wind-borne 33, mostly *Compositae*; Ferns 44; of small-seeded plants, possibly borne in mud on birds' feet or feathers, 31. Dubious are *Zanthoxylum*, *Collettia*, *Margyricarpus* (fruit a dry achene), *Escallonia*, *Eryngium* (2), *Selkirkia* (*Boragineae*), endemic with winged and toothed nutlets. The presence of *Oxalis* is comparable to the case in Fernando de Noronha. The fruits, I suppose, are bird-eaten. The number of species in the genera of endemics is larger than we are accustomed to in oceanic islands: *Robinsonia* (6), *Dendroseris* (7) (*Compositae*), *Wahlenbergia* (*Campanulaceae*) (4).

San Ambrosio and San Felix are 450 miles from the Chile coast. They are small islands with a scanty flora. Bird-dispersed: *Sicyos* (*Cucurbitaceae*); adhesive, probably *Malvastrum limensis*, with prickly carpels, *Atriplex*, *Parietaria*, *Heliotropium stylosum*, perhaps adhesive to birds' feathers or feet; *Apium* sp., perhaps sea-borne; *Lycapsus*, *Dendroseris* and *Thamnoseris* (*Compositae*) fruit plumed, probably wind-borne.

Galapagos Islands.—These are 600 miles from the coast of South America. There seems to be little doubt that these are continental islands formerly connected with South America. They possess an extensive flora of American affinity, a large number of endemic species, and a considerable addition of obviously introduced plants, and the species are numerous in proportion to the genera. Of sea-transport plants there are about 27 species. Wind-dispersed: several plumed Composites, a *Tillandsia*, 4 Orchids, 75 species of Ferns, 5 *Lycopodiaceae*, and an *Equisetum*.

Of drupaceous plants about 50, including 2 *Oxalis* and 10 *Cactaceae*. Of adhesive-fruited plants about 36, and a number of plants whose small seeds and fruits might have been (and in some cases doubtless were) brought on birds' feet. There had been some amount of human colonising, and cattle had been introduced and run wild, and were doubtless responsible for the introduction and dispersal of some of the plants. The burrs of a *Triumfetta* were found, by one of the American expeditions, attached to the hair of one

of these wild cattle. There are many sea-birds and waders, 5 kinds of heron, 3 ducks, 1 dove, 2 rails, and 14 finches, visiting and resident on the islands.

Cocos Island.—This island is 360 miles from Costa Rica. The flora is not thoroughly known, but A. Stewart has given an account of what has been collected there. There are 18 species of drupaceous or baccate fruits which may have been introduced by birds. Of those whose fruits are adhesive to feathers we may reckon *Chloris* (1 endemic) and a *Peperomia*. Of wind-dispersed plants, a *Tillandsia* (doubtful), 17 Ferns and 1 *Lycopodium*. Dubious small-seeded plants are 5 *Cyperaceae*, *Cecropia*, *Acalypha* and *Clibadium*, *Rolandra* (possibly adhesive), and *Wedelia paludosa* (*Compositae*). There has been a Settlement on the island, and some obvious weeds are recorded. Stewart points out that there are nearly as many species as genera, showing a great contrast with the flora of the Galapagos, which suggests its being a true oceanic island.

SUMMARY.

The real value of the study of island floras consists in its showing the effects of plant dispersal by certain limited means, and the distances at which those means are effective. Sea-borne fruits and seeds can reach every island and coast in the world. The absence of such species is due to the unsuitability of the coast on which the seeds land, either for climatic reasons, or from the absence of sand or gravel beaches where the plants can grow. Islands like South Trinidad, St. Helena, and Christmas Island to a large extent, where the rocks descend straight into the sea, are naturally unfurnished with beach plants. Wind-dispersed plants have a more limited dispersal distance, except in the case of Sporophytes. The rapid decrease in numbers of plume-seeded or plume-fruited plants according to distance is well illustrated by the numerous plume-fruits of Krakatau, a flight of 25 miles, and the scanty number in Christmas Island, 120 miles farther away from Java. Plume-fruits are characteristic of continents, and when there are a great variety of indigenous species on an island, we may suspect that the island is continental, a detached portion of the adjacent land.

Dust-seed plants, Orchids, *Balanophora*, etc., though occurring on almost all islands, even at a distance of 700 miles (Hawaii, South Trinidad), are least abundant at these long distances. They gradually diminish as the distance lengthens. Sporophytes have no limit for the dispersal of their spores, and are only absent from localities too dry or cold for the development of the plants. Plants dispersed by birds occur in most islands. In some, where frugivorous birds are absent, there are no drupaceous or baccate fruits, as in South Trinidad, St. Helena, Cocos-Keeling and many of the Antarctic islands; but where there are sea-birds, there are always a certain number of plants whose seeds or fruits can be attached to their feathers, while waders, ducks and herons bring seeds attached to mud on their feet. Pigeons and thrushes seem to be the most important of the birds to convey seeds to remote islands internally, but their limit of flight appears to be under 700 miles over sea.

The action of mammals (exclusive of fruit-bats, in tropical Asia) is absent. They play an important part in continental distribution, and the presence of plants habitually dispersed by them on a group of islands is some evidence that the island was formerly attached to the mainland.

Most of the islands in the world have been settled on or at least temporarily visited by man, who invariably brings with him some of the well-known weeds. Mere shipwrecks add very little, if anything, to the local flora, but a settlement, however short, brings additional plants, and even expeditions have

been known to do so. In the cold climates the first aliens to appear, introduced by man, are *Sonchus oleraceus*, *Poa annua* and *P. pratensis*, *Stellaria media* and *Plantago major*, probably brought attached to baggage. The introduction of cultivated plants and cattle vastly increases the number of aliens. Ever since the evolution of man and the invention of sea-travel, man has wandered about the world from one island to another, carrying plants with him, so that the original home of many plants common as weeds is now unknown. The absence of weeds from any island and in many continental localities is some proof that man has never settled there.

An island, when newly formed, is furnished with vegetation principally at first by wind, then by sea-currents, later visited by sea-birds with seeds attached to their feathers. Many islands, especially coral atolls, are not supplied by any further additions. When the trees whose seed has been brought by the sea are sufficiently large, wandering frugivorous birds may reach them, and bring seeds of drupaceous or baccate plants, and waders, herons, and ducks may visit them and bring the small seeds of shore and marsh plants, and the adhesive fruits of *Boerhaavia*, *Triumfetta*, *Pisonia*, etc. Later the island is occupied by man, and the flora is (so far as is possible) completed.

One characteristic of an oceanic island flora is that the number of species is little more than that of genera. Of most of the genera there is but 1 species, but occasionally there are 2 or 3, and this even in islands of great antiquity, as in Christmas Island, where we find 2 species of *Abutilon*, 2 *Laportea*, 2 *Ficus*, 2 *Peperomia*, etc., but no more, and Fernando de Noronha, 2 or 3 *Cayaponia*. There is no doubt that these islands have been long above water. Indeed, Christmas Island is reported to have been of Eocene age.

Where we have genera of 6 or 7 species we may be suspicious of their being continental islands, detached portions of a larger land surface, and the presence of plants which have no facilities for crossing the sea confirms this. The actual number of species on an oceanic island is also very much smaller than on a continental island. I was very much struck with this in Christmas Island. After about a week, I and my plant collector, in our long tramps through the forest, hardly added a new plant to our collection, while in a continental island, e.g., Java, we should have procured 20 or 30 a day.

CHAPTER XII

DISPERSAL OF ORDERS AND GENERA

Small-Seeded Plants of Wide Distribution Not Bird-Dispersed—Widely-distributed Species—Variation in Method of Dispersal in Allied Plants.

If we examine the orders of flowering plants from the view of their dispersal agents, we are first struck by the very large proportion of their constituents which possess baccate, drupaceous, or arillate fruits, evidently modified for dispersal by frugivorous birds, assisted to some extent, in the tropical regions, by fruit-bats. In many orders practically all the species are adapted for dissemination in this way, though not infrequently cases of dispersal by wind or water occur in addition. When we add to these the numerous plants in which the seeds are known to be dispersed by their adhesion to the feet of birds and mammals in mud, or in which the fruit or seed is adherent by hooks, spines, or viscidity, and those in which the seeds are accidentally swallowed by herbivorous mammals in feeding on foliage, and the jungle stone-fruit eaten by the larger mammals, we see at once what a vast difference to the evolution of the innumerable species of plants now forming the flora of the world is due to the evolution of the mammalia and birds.

At what geological date this evolution commenced seems as yet uncertain, but it is probably not later than the Lower Cretaceous Period. In the Eocene Period there were, it is clear, a very large number of plants with baccate and drupaceous fruits, connoting the presence of abundance of frugivorous birds, although few, if any, traces of this part of the fauna have yet been met with.

Besides whole orders in which the seed-dispersal is almost entirely or completely due to birds, there are hardly any other large orders in which some genera are not disseminated in this way. Thus in the usually wind-dispersed *Orchidaceae* we have the widely-dispersed baccate *Vanilla*; in *Compositae*, *Wulfia* has drupaceous black achenes; in the *Labiatae*, *Gomphostemma* has white fleshy nucules; in *Leguminosae*, the pulpy *Dialium* fruit; in *Cyperaceae*, *Scleria sumatrensis* has a red fleshy disc, and so on.

The following are the orders of which the species are exclusively, or almost exclusively, disseminated by frugivorous birds, often aided by fruit-bats and other mammals.

Anonaceae (except *Anaxagorea*), *Dillenia* (except *Hibbertia* and *Acrotrema*), *Magnoliaceae*, *Menispermaceae*, *Guttiferae* (mainly), *Schizandraceae*, *Pittosporeae*, *Flacourtiaceae*, *Ampelideae*, *Ilicineae*, *Cactaceae*, *Cucurbitaceae* (mainly), *Passifloraceae*, *Larzibalaceae*, *Araliaceae*, *Cornaceae*, *Sapotaceae*, *Ebenaceae*, *Myrsineae* (except *Aegiceras*), *Salvadoraceae*, *Styraceae* (except *Halesia*), *Laurineae*, *Elaeagnaceae*, *Myristicaceae*, *Loranthaceae*, *Piperaceae* (except *Zippelia* and *Peperomia* with adhesive fruits), *Chloranthaceae*, *Empetraceae*, *Moraceae* (except *Dorstenia*), *Zingiberaceae*, *Musaceae*, *Liliaceae*, section baccatae (with some capsular-fruited ones, as *Peliosanthes* and *Gloriosa*, with coloured pulpy testa), *Palmaceae* (except *Nipa*, *Cocos nucifera* and a few others), and *Flagellariaceae*.

Among the widely-distributed genera, of which almost all the species are bird-dispersed, and which are found spread over the north temperate zone and tropics in both hemispheres, we find the following :—*Magnolia*, *Tetracera*, *Berberis*, *Mahonia*, *Sterculia*, *Grewia* (tropics only), *Ilex*, *Euonymus*, *Celastrus*, (absent from South America), *Salacia*, *Rhamnus*, *Vitis* (including *Cissus*), *Rhus*, *Prunus*, *Pyrus*, *Crataegus*, *Rubus*, *Fragaria*, *Rosa*, *Ribes*, *Eugenia* (tropics), *Myrtus*, *Casearia*, *Passiflora*, *Cornus*, *Nyssa*, *Sambucus*, *Viburnum*, *Lonicera*, *Vaccinium*, *Gaultheria* (absent from Europe), *Myrsine*, *Ardisia*, *Chrysophyllum*, *Sideroxylon*, *Diospyros*, *Symplocos* (absent from Africa), *Linociera*, *Menyanthes*, *Solanum*, *Piper*, *Myristica*, *Beilschmiedia*, *Cinnamomum* (extinct in Europe and America), *Elaeagnus* (absent from Africa), *Loranthus*, *Viscum*, *Trema*, *Celtis*, *Ficus*, *Laportea* (absent from Africa), *Myrica*, *Empetrum*, *Vanilla*, *Smilax*, *Polygonatum*, *Sabal* (formerly Europe, now American only).

Among these bird-dispersed genera are some of those possessing an unusually large number of species. Thus *Eugenia* has approximately 900 species, *Ficus* 600, *Rubus* 430, *Vitis* (including *Cissus*, *Ampelopsis*, etc.) 400, *Ilex* 270, *Ardisia* 235, Rhus 113, *Vaccinium* 100. Species of *Eugenia*, *Ficus* and *Vitis* occur in almost every island warm enough for them, and in the tropics are conspicuously abundant in individuals.

Orders exclusively, or mainly, of plants whose seeds are dispersed by the action of wind are comparatively scarce in flowering plants, but practically all the Cryptogams, vascular and cellular, are so disseminated. Among flowering plants we have *Orchideae* (all but *Vanilla*), *Begoniaceae*, *Asclepiadaceae* (except *Sarcolobus* and *Finlaysonia*), *Bignoniaceae* (except *Crescentia*), *Platanaceae*, *Nepenthaceae*, *Salicaceae*, and *Casuarinaceae* (*Casuarina equisetifolia* also by sea). Among large genera we have *Senecio* with 3,230 species, dispersed over the whole world; *Bulbophyllum*, 1,438 species, dispersed over tropical Africa, Asia, Polynesia, and South America; and *Begonia*, over 1,000 species, very widely spread, but in this genus the plants, being unisexual, hybridise extensively, and many of the described species may be natural hybrids. *Rhododendron*, abundant in the north temperate region and extending to the tropics, contains about 974 species. It is absent from islands. The wind-dispersed reed *Phragmites communis* is the most widely-disseminated plant in the world, and *Taraxacum* and *Sonchus oleraceus*, though aided in their migrations by man, owe a good deal to the wind in their distribution, now nearly all over the globe.

Orders entirely, or mainly, dispersed by water are: *Hydrocharidaceae*, *Naiadaceae*, *Potamogetonaceae*, *Lemnaceae*, *Ceratophyllaceae* and the *Rhizophoraceae*, and also the marine *Algae*, but the first 5 owe much of their dispersal to the adhesion of their fruits or seeds or portions of the plants to water-fowl. Most of the genera are small, *Potamogeton* being the largest with 87 species, and probably the world-wide *Ruppia rostellata* is the most widely distributed. The *Rhizophoraceae*, though few in numbers of species, are as widely distributed as their environments and requirements permit.

Orders of which the species are disseminated by explosion of the capsule exclusively, or almost so, are the *Balsaminaceae* and *Acanthaceae*. *Impatiens* is a widely-dispersed genus, occurring in both hemispheres, with about 640 species.

Small-Seeded Plants of Wide Distribution Not Bird-Dispersed.

There is a certain class of small-seeded herbs which appear to have originated in the temperate regions (Palaearctic), and to have spread very widely into the tropics, though they are almost confined to the cooler mountain ranges. These plants have, apparently, no means of diffusion to long distances across extensive plains or the arms of the sea. They do not frequent marshy land or seashores

where waders or ducks haunt. They may be disseminated to short distances by wind and by rain-wash.

Such genera are *Viola*, *Polygala*, *Hypericum*, *Ranunculus*, *Anemone*, *Gentiana*, *Primula*, *Rhododendron*. This latter has, however, very light seeds, which might travel nearly as far as those of *Orchids*. Except *Ranunculus*, in the Antarctic region, they are conspicuously absent from islands; *Ranunculus*, however, grows, in these cases, in marshy land, and is often adhesive by the style.

When we look at such plants as the tiny *Gentians* of mountains of Java and of Gunong Tahan in the Malay Peninsula, which are closely related to some of the Himalayan species, we may safely assume that the minute seeds of these isolated plants could not have been carried by the wind from the top of one mountain to the other, across miles of sea, but rather that in a former era these mountains were connected by ranges long swept away by denudation. The story of this class of plants belongs rather to the history of past changes in land surfaces than to questions of dispersal.

The genus *Carex* has been studied, in the matter of its distribution, carefully by Guppy in "Plants, Seeds, and Currents." It is remarkably widespread, and 800 species are recorded. Though mainly inhabiting temperate regions, they are by no means rare in the tropics, and are represented in many of the islands of the temperate areas. Guppy points out that the seeds are sometimes found in birds' stomachs, and may be easily transported in mud on their feet. *C. baccans*, rather widely distributed in the East Indies, has fleshy utricles of a conspicuously red colour, which may be eaten by birds. No doubt many species are distributed by adhesion to the feet of birds, and some, perhaps, by adhesion of their hairy utricles to their feathers; but I am not satisfied that their wide distribution, occurring as they do in the dense forests of, say, the Malay Peninsula, can be accounted for by any of these ways. Most of the widely-distributed plants, whose seeds are transported by birds in mud on their feet and feathers, are mud or marsh plants, e.g., *Scirpus*, *Montia*, *Jussiaea*, *Polygonum*, *Tillaea*; but many of these *Carices* are not inhabitants of spots where the wading birds ever go, nor can be accounted for by their fruits being river-borne. The question is simpler with the large genus *Cyperus* (including *Pycreus* and *Mariscus*), which to some extent replaces *Carex* in the tropics. The number of species included under it is 562. Of these, a considerable number owe their distribution—often very wide—to human action; some few, e.g., *Mariscus albescens*, *M. atlanticus*, etc., are sea-dispersed. They are remarkably scarce in the high forests of the tropics and from the high mountain regions, in both of which districts one often meets with *Carices*. In marshes, river banks, and places where wading birds can go, they are largely represented, and in such places are, no doubt, transported on the feet of marsh birds and perhaps mammals, but many occur in open dry spots where this factor is absent. In such spots as the dry, open heath country (matto) of Brazil, and the veldts of Africa, they are very abundant. The same remarks apply to the genera *Fimbristylis*, *Scirpus* 100 species, *Rhynchospora* 189, *Cladium* 65, and the *Eriocaulons*—so abundant on the Brazilian matto—350 species. These little herbs seem to get about the world with much ease, although, with the exception of a few obviously transported on birds' feet or feathers, there seems no reason why they should be so widely spread. They are mostly continental and not insular plants. Some of the plants which accompany them in marshy or wet spots, *Polygonum* with 100 species, *Drosera* 84, and *Jussiaea*, *Montia*, *Tillaea*, all very widely-distributed genera, are certainly largely dispersed by birds and water-rushes, but I do not think that this is sufficient to account entirely for their wide distribution.

Widely-Distributed Species.—There is, of course, a great variety in the areas of distribution of species of flowering plants. A good many extend all

over the Palaearctic and Nearctic zone, but no further. Plants of the seashore, like *Ipomoea biloba*, are drifted as seeds all over the tropics, but though the seeds drift into the northern regions, they fail to establish themselves. The *Calystegias*, *C. sepium* and *C. soldanella*, originating in the Antarctic area, migrated apparently along the American coasts to the Palaearctic area, where they became common; but though it appears they must have passed through the tropics, they have ceased to exist there now.

The most widely-spread species of flowering plants is the common Reed, *Phragmites communis* (including the smaller-spikeleted form, *P. Karka*). It is a plant of the temperate regions which has pushed down from the north in both hemispheres nearly to the south.

This is a continental plant, only absent from part of Australia and the extreme south of America, and from oceanic islands. It arrived, however, very early in Krakatau after the eruption.

Its plumy spikelets are easily transported by wind, and possibly by adherence to the feathers of birds which have lined their nests with them. It may also migrate to some extent by drifting pieces of rhizome, which, however, perish very soon in the sea. It possesses thus a good dispersal mechanism for considerable distances (25 miles at least at a time), an adaptability to cold or hot climates, and a habitat in marshy or river-bank land, ponds and wet seashores, which suitable habitats for it occur all over the world.

Cynodon dactylon, a very widely-spread grass, is a tropical sandy ground plant which has spread into temperate regions. It seems unable to endure severe frosts, but localities with mild winters, as at Studland Bay, Dorset, and Penzance, Cornwall, suit it fairly well. It has no very definite means of transport beyond what might be effected by the wind rolling or blowing the grains along, and by rain-wash, possibly also to some extent by cattle feeding on it and passing the seeds. In some places human action has come into play, but this will not account for its wide distribution. It, like the Reed, is continental, and rarely, if ever, reaches distant islands. It is largely a desert plant, and can grow in hot sandy spots, but very soon disappears in damp ground. *Eleusine indica* is another grass of very wide distribution, but I think that is largely due to accidental transport by man, through his cattle.

Now follow a number of small-seeded marsh plants which we know, or have reason to believe, are dispersed in mud on the feathers or feet of marsh and shore birds. These are *Montia fontana*, *Polygonum hydropiper*, and perhaps *P. lapathifolium*, *Ceratophyllum demersum*, *Scirpus maritimus* and *Sc. lacustris*, and *Ruppia maritima*.

Montia fontana (*Portulacaceae*), a very small marsh plant with minute seeds, ranges from the northern Arctic region all over Europe, and temperate Asia to Japan, and from North America to the Falkland Isles, from South Georgia to Macquarie, Campbell, Kerguelen, and the Auckland Isles. It is absent from Africa, except Morocco (a closely allied, if not identical, plant found on Kenya), and from the whole of tropical Asia, the Canaries and Azores. This distribution can only be associated with dispersal on the feet or feathers of one of the marsh birds, or perhaps, in the Antarctic islands, of sea-fowl.

Polygonum hydropiper and *P. minus* are also widely-distributed marsh and stream bank plants, the achenes of which are disseminated by adherence to the feet of birds. They occur in Europe, Asia, India, Malay Peninsula and Islands, Australia, New Zealand and Chatham Islands (*P. minus*).

Ceratophyllum demersum, with its small spiny seeds readily attached to the feathers and feet of birds, is practically distributed all over the world where there are ponds or lakes suitable for its growth, from Iceland to Australia and Fiji, Africa and America, and the Azores.

Ruppia maritima is another world-wide aquatic found on the coasts

of Europe, Asia (India, China, Formosa), Malay Peninsula, Philippines, South Africa, Socotra, Canaries, Madeira, Mauritius, Australia, New Caledonia, New Zealand, all America and West Indies, including Bermudas, probably mainly dispersed by ducks.

Scirpus lacustris and *Sc. maritimus* also are plants of practically world-wide distribution, whose small achenes are readily carried about by their attachment in mud to birds' feet. *S. lacustris*, a slow-moving river and swamp plant, and *S. maritimus*, requiring more or less brackish water, are only absent from the equatorial region. Two plants with adhesive fruits have a very wide distribution, the Sanicle (*Sanicula*) and the Clot-bur (*Xanthium strumarium*). These are both mainly continental, being dispersed by adhesion to the fur of animals, but the Sanicle is found also in the Azores and Hawaii, where it was doubtless transported by birds. *Xanthium* has undoubtedly been aided in its wanderings by man to some extent, but it apparently owes the greater part of its distribution to the adherence of its fruits to the fur and wool of animals.

Though plants with drupaceous or baccate fruits are generically and ordinally widely distributed, species of this class of plant are comparatively of local distribution. *Empetrum nigrum* is very widely distributed, and replaced by *E. rubrum* in the southern hemisphere; being plants of temperate open heathy districts, they are absent from the tropics. The Juniper (*J. communis*) and the Yew (*Taxus baccata*) have also a very wide distribution, though they are also limited by their climatic requirements.

Pteris aquilina is the most widely distributed of ferns, but is also continental, being absent from islands. Its light spores are very readily borne about by the wind, as are those of all ferns, but it is also to some extent accidentally spread by man.

There is no reason why ferns whose spores are so light should not be more widely distributed than they are, except their limitations due to requirements for humidity, especially in the prothallus stage. Some of the most widely-distributed ferns, *Trichomanes radicans* and *Angiopteris evecta*, are evidently remains of the old fern flora; *Ceratopteris thalictroides*, a ditch plant, has the spores, perhaps, borne about by water-fowl, and *Acrostichum aureum*, a tidal-swamp fern of wide distribution, have no fern competitors in their peculiar habitats.

Variation in Method of Dispersal in Allied Plants.—It has been shown that in some orders all the plants have fruits or seeds destined to be dispersed by one method only, but in many large orders, and some of the smaller ones, plants are found which have the seeds disseminated by several methods and adaptations, and even plants of the same genus not infrequently have different methods. I give some examples of the different modifications in large widely-distributed orders:—

In *Leguminosae* we have WIND-DISPERSED fruits and seeds: *Dalbergia*, *Albizzia* (samara), *Sutherlandia*, *Colutea* (bladder fruit), *Trifolium* (corolla-winged).

WATER-DISPERSED: *Sutherlandia*, *Colutea* (bladder fruit), *Derris uliginosa*, *Pongamia* (sea-dispersed), *Neptunia*, *Aeschynomene* (stems floating), *Lathyrus maritimus*, *Guilandina* (seeds floating).

ANIMAL-DISPERSED: *Dialium*, *Tamarindus*, *Mezzettia* (by mammals), *Acacia* spp., *Prosopis* (pods eaten by ungulates), *Cassia goratensis*, *Afzelia cuanzensis*, *Sindora* (aril of seed eaten by mice), *Acacia cyclops* (aril eaten by birds), *Adenanthera* (false arillate seeds swallowed by birds), *Ulex*, *Sarothamnus*, etc. (Elaiosome eaten by ants), *Medicago*, *Desmodium*, etc. (adhesive pods to animals), *Sindora*, *Smithia* (adhesive to feet by spines), *Clitoria cajanifolia* (seeds adhesive by viscidity), *Vicia*, *Lotus*, *Bauhinia* (seeds dispersed by explosion).

The extraordinary variety of methods of dispersal in the order *Amarantaceae* is illustrated by G. Lo Priore in "Biologie della *Amarantacees*" (Contrib. Alla Biologie Vegetale par Borzi, iii, p. 316), who gives the following list, to which I have added some :—

BIRD-DISPERSED (fruits baccate) : *Deeringia, Bosia, Pleuropetalum.*
Fruits adhesive by spiny bracteoles : *Centema, Acanthochiton.*
,, ,, sepals spiny : *Centrostachys, Nyssanthes.*
,, ,, sepals : *Aerua.*
,, ,, sepals and bracts : *Achyranthes.*
,, ,, style and stigma : *Celosia, Hermbstaedtia.*
,, ,, sterile flowers : *Cyathula, Pupalia, Centema, Kentrosphoera, Dasysphaera, Digera.*
FRUITS EATEN BY CATTLE, ETC., AND SEEDS PASSED : *Amaranthus.*
FRUITS DISPERSED BY WIND :
Bracts large, wing-like : *Gomphrena, Cristularia, Marcellia.*
Sepals wing-like : *Amaranthus Micheli, Froelichia, Alternanthera sessilis.*
With hairy appendages : *Stilbanthus, Iresine.*
Sterile flowers, winged : *Pleuropteranthera.*
,, ,, pilose : *Sericostachys.*
SEA-DISPERSED BY BRANCHES, ETC. : *Philoxerus vermicularis.*
In *Malvaceae* we have :—
WIND-DISPERSED BY PLUMED SEED : *Bombax, Eriodendron.*
SEA-DISPERSED : *Thespesia, Hibiscus tiliaceus.*
FRUIT EATEN BY MAMMALS AND BIRDS : *Durioneae, Adansonia.*
In *Araceae* :—
BIRD-DISPERSED : *Arum, Amorphophallus.*
SEEDS, RIVER-DISPERSED : *Typhonodorum, Aglaodorum.*
SEEDS DISPERSED BY RAIN-WASH : *Colocasia.*
RHIZOMES DISPERSED BY RIVER : *Acorus.*
BULBILS ADHESIVE : *Remusatia.*

These are examples of variation of dispersal methods in orders. Many more might be added. Besides those, we have plants of the same genus diversely disseminated, as *Derris thyrsiflora* by wind, *D. sinuata* and *D. uliginosa* by sea-dispersal. In the genus *Acacia* we have some in which the pods are dispersed by wind, some eaten by mammals and the seeds evacuated, one almost certainly sea-dispersed to some extent (*A. Farnesiana*), and one or more with funicular aril eaten by birds ; *Marrubium deserti* is wind-dispersed, *M. vulgare* by adhesion of the calyx to rabbits' fur, some species of *Geum* by adhesion to animals' fur, and some by plumed style wind-dispersed.

Frequently, too, we have cases of the same species disseminated by different methods, as in *Capsella Bursa-pastoris*, which is dispersed by the wind blowing away the seeds after dehiscence of the capsule ; by the seeds being dispersed by rain-wash ; by their being swallowed by cattle, yaks, etc., in eating the whole plant ; by birds swallowing the seeds ; by adhesion, etc., the seeds being mucilaginous ; and by human agency. *Hordeum murinum* is dispersed by wind, rain-wash, adhesion to cattle and human clothing. Wide dissemination of a species is not necessarily due to a variety of methods of dispersal, though undoubtedly a plant benefits greatly by having more than one method. A single adaptation for dissemination is often quite sufficient to establish a plant as an abundant and widespread one, as we have seen in *Epilobium angustifolium*, wind-dispersed ; *Ipomoea biloba*, sea-dispersed ; and *Empetrum nigrum*, bird-dispersed. Adaptability to varied environments or the large extent throughout the world of the particular form of environment suited for a plant is the most important factor in the world, and this is especially so when these conditions are so specialised that the plant has few competitors.

CONCLUSION

Change of Environment—Evolution of Methods and Apparatus for Dissemination.

THE advantage of dissemination to a species lies in the diffusion of the seeds so widely that a sufficient number may reach suitable spots where they can go and reproduce the species, and so carry on its continuance. Should they fail to do this, the species would, after a time, cease to exist. The plants which we see now in the world are those which have succeeded in doing so. Plants which are able to maintain themselves, and propagate freely under different circumstances and environments, become what are known as common plants, wides, or cosmopolitan plants. They are the most successful ones in the struggle for existence.

The primary use of dissemination is to scatter the seeds away from the mother-plant, to fall or be carried clear of foliage and of close competition, and to prevent their growing so close together that pests, animal or vegetable, shall not be able to accumulate and destroy them. Local environment frequently changes; indeed, it may be said that environment conditions are constantly becoming altered on a small or large scale all over the world, and this has always been going on.

Usually a plant produces a very large number of seeds, of which far the greatest number perish, only a few surviving. These survivors are those that have successfully reached a spot where, from lack of competition, they can continue to reproduce the species. The number of seeds produced at a time by a plant, whether small or very large, has little bearing on the abundance of the species: an Orchid may produce a vast number, and be rare; a Composite, like the Dandelion, comparatively few, and be abundant.

In some cases, as has been shown, suitable methods have been adopted to arrest the seed in its wanderings at a suitable spot for the development of the plant; but in many cases a large number of seeds are wafted about on the chance that some will quite accidentally reach the suitable locality. Either system is efficacious. To some extent (as in fishes) the production of vast numbers of young, most of which are destined to become failures, occurs among animals; but the higher animals produce a smaller number of young, most of which live long enough to reproduce the species. The migrations of animals are voluntary, and for the most part effected by adults. Adult plants seldom migrate, their wanderings being carried out in the embryonic state of the seed. Depending as they do on the irregular actions of wind, water, or animals, it is necessary that large amounts of seeds should be produced in order that some may be safely planted.

In most large areas we have a number of local species confined to a limited spot. Some of these are species in the course of evolution, which may eventually spread (endemic); others are relics of a perished flora, which, by change of environment, remain isolated, unable to spread farther, they are destined sooner or later to disappear, as so many have done before; these are epibiotics. But far the largest number of plants extend over wide areas of various dimensions, only checked in spreading more widely by competition

and by unsuitable environments which they cannot cross. The fewer wide-spread species, which are cosmopolitan, are those which are more tolerant of changed environment, or which find widely-stretched areas of the most suitable circumstances for them, and which can cross any barriers by means of an adequate dispersal method.

The distance apart at which plants of one species can grow varies very much according to the size of the plant and its root area. Small herbs, like the daisy, often grow successfully very close together; big trees require a space of about 30 yards apart, so that, to be successful, the seed-dissemination must be as far as is necessary for development. The continuous change of environment constantly comes in, whether it be on a large or small scale. There is a perpetual fight between the various plants for suitable growing spots. A seed may fall on a bare spot and develop into a plant, but be surrounded by competitors, when it has to struggle with numerous other plants for root-space and light, and in many cases also for water. Its descendants must move on elsewhere, or the plant perishes from that locality.

In spots where the environment is unsuited for most of the invading plants, a species may hold its own for many years, perhaps centuries, without being able to cross the environment barriers. That is why so many epibiotics are found on rocks or precipices, as is the case in *Gesneraceae* of Europe, *Boea* on the cliffs of Selangor and the Borneo mountains, the sea-coast *Pisonia* and seashore *Cycads* in the Perak forests. Isolated by a complete change of flora, they are unable to cross the environment barrier, and remain, just maintaining their position, in a spot for climatic reasons unavailable to the surrounding modern invading flora.

The age or long duration of a species unaltered has little or nothing to do with its area of distribution. It is true that we occasionally find plants in two areas far apart now which are the relics of a long past period in which the two areas were connected, though perhaps thousands of years have elapsed since the sea first rolled over the intervening land; or the connecting mountain chains along which the plants spread have been denuded away, leaving the plants in isolation. Such plants are *Eriocaulon septangulare* of Western Ireland and Scotland and of North America; the *Arbutus* of Portugal and Killarney; *Engleranthus* of Ceylon and Kenya mountains, etc. But these are comparatively few in number. In most cases widely-distributed plants are commonly either modern species or their wide travels are those of modern times, while often quite local species of very limited area now (we know from palaeobotany) were at one time very widely spread, as is the case in the genera *Platanus*, *Nipa*, *Cinnamomum* and *Stratiotes*.

Many of the ferns and cellular cryptogams, which we know to be very old groups, are widely spread; but this is clearly due to their exceptional facilities for wind-dispersal and their adaptability to varied environment, not to the long period which has elapsed since they were first evolved.

Facility of dissemination over long distances, and adaptability for a varied environment, or the occurrence of suitable spots for growth over extended areas, are the factors of distribution. Without these two factors, plants cannot migrate, and with change of environment, unless they can become so modified that they can adapt themselves to the change, they must completely perish.

Change of Environment.—The greatest change of environment over a large area since the Glacial Period is the one due to the evolution and consequent actions of man, who has, locally at least, exterminated many species, or reduced them in number, by agriculture, drainage of swamps and lakes, and destruction of the forests for timber and planting, and has substituted plants of one area for those of another. Over large areas he has transformed the original forest and swamp soils into garden soil, suited for an entirely new

class of plants, which in many cases have been imported from far distant continents to their new home. This change of environment has been more or less continuous for about 8,000 years in some parts of the world, but its rapidity has been much increased in the last two or three centuries. The competition of plants to occupy this new class of agricultural soil has been much aided by specialised methods of dissemination. Over all this altered ground there has been a constant rain of seeds of all kinds, but the first to establish themselves have been those possessed of the best methods of dispersal, as well as a suitability for growth under the new conditions.

Two factors are required to re-cover ground cleared by man or Nature, or, rather, partly cleared, for even in the great sweep of ice southwards, during the Glacial Period, the whole flora was not completely destroyed, some plants persisting in warm corners. These two factors are :—sound methods of dissemination and adaptability to changed environment. To form a new flora, both of these factors must work concomitantly. The latter factor, which has not yet been adequately studied, I have not attempted to elucidate. I have dealt only with the former. Changes of climate, which are also continuous in many parts of the world, though usually slow, play an important part in transforming a flora ; an alteration in the rainfall may be due to the destruction of forests, which may be caused by the denudation of mountain ranges. This I have pointed out in the earlier part of the work. It may have a strong effect on the part of the fauna important for dissemination, as the hairy mammals, the ungulates, the frugivorous birds, may increase or diminish in numbers, and the plants with adhesive seeds or fruits, or with drupes or berries, may concomitantly rise or fall in number, and in some cases many may disappear. Unless, as often happens, the fruits are modified for another form of dissemination, the species perish, and that vast numbers have perished there is no reason to doubt. We know this from the number of fossil plants whose remains are found in various strata, and also from facts in the distribution of plants. We find a small species of *Argostemma* (*Rubiaceae*), a little jungle herb, confined to Western Africa. It belongs to a set of plants which has no means of dissemination except for short distances by rain-wash. A nearly identical plant is found in North India, but nowhere between these two localities could it survive in the now dry hot area lying between these two places, 5,500 miles apart. It, with a few other species, are all that remain of a continuous flora formerly occupying this great extent of land. This is, of course, only an isolated example to show what a vast number of plants must have disappeared from changes of climate and other factors of environment throughout the world. All students of the distribution of plants will be acquainted with many other similar cases.

A real clean sweeping away of the whole flora of a large area does not seem to be a very common occurrence. We have had this on a small scale on the island of Krakatau, on a large scale in the Glacial Period, in the sweep of the desert sand over the Sahara, which appears to have been formerly heavily afforested, and in the great destruction by man of the original forest floras of India and Ceylon ; but in most of these cases a certain number of the original species occupying the ground have adapted themselves to the change. Very few of the pre-Glacial plants which formerly occurred in the British Islands entirely disappeared during the Glacial Period. They are *Acer monspessulanum*, *Trapa natans*, *Salix polaris*, *Picea excelsa*, *Naias graminea* (accidentally reintroduced in one spot), *Naias minor* and *Hypecoum procumbens*, while *Brasenia*, known fossil in Europe, has also long disappeared from there. Many plants, however, common in Britain in pre-Glacial periods, are now scarce. Even in areas which man has put under cultivation and abandoned, a mixture of the relics of the original flora with introduced weeds is the usual flora found. But it is

not only in completely cleared areas that the dissemination factor comes into work. Plants, as I have shown, become adapted, by dispersal methods, to push themselves into vacant spaces, to become so modified that they can occupy positions which were previously forbidden to them. I have called attention to the *Labiate Gomphostemma*, and some species of *Hedyotis* (*Rubiaceae*), open-country plants which have forced their way successfully into deep shady forests, and how *Dolichandrone Rheedii*, from a forest and freshwater river-bank habitat, has accepted a tidal mud and sea-coast home, the result being that these plants have become successful, abundant, widely spread, and thriving in spots where their unadapted relations were not able to penetrate.

Many of the weeds of cultivation were probably at first local and scarce, but being adapted for growth in agricultural soil, and having been transported there by human aid, and possessed of some good means of dispersal, are now become what the old botanists used to term "cosmopolitan," occupying all corners of the globe where climate permits, and becoming very abundant there.

While adaptability to environment is of the greater importance to a plant in its migrations, it would be useless to the species unless it also possessed a good dispersal mechanism, in order to reach the spots suited for its growth. The most successful plants are those that possess both in the highest degree.

Evolution of Methods and Apparatus for Dissemination.

As I have shown in several parts of this work, wherever we have a fairly complete series of species or genera, we see that the various modifications for dispersal are gradually evolved from some organ or modification, or condition of an organ which has preceded them, and has generally been utilised for a different purpose. The evolution of adhesive hooks or spines from hairs originally serving to reduce the transpiration of water, or to protect an ovary from injury by raindrops, and, when necessary, the evolution of the adhesive apparatus into a flying organ, or *vice versa*, are examples. I have shown in one place the evolution of a 4-winged fruit wind-dispersed to short distances, by the gradual lengthening of the wings and the reduction of the body, and the lessening of the number of wings from 4 to 2, to the ideally adapted long-distance wind-transported fruits. We have seen the scarlet fruit of *Sterculia*, with its contrasting blue-black seeds, beloved of birds, transformed to the thin boat-shaped 1-seeded carpels of *Scaphium*, wind-borne in the forests, where frugivorous birds are scanty, and this, in turn, by the enclosing of the seed in a thick corky part of the carpel, into the river-dispersed *Heritiera fomes*, and again, by greater thickening of the pericarp and total disappearance of the wing, into the sea-dispersed *Heritiera littoralis*, concomitantly with the adaptation of the plants from inhabitants of the dry forest to the permanently wet mud of the river bank, and from the freshwater river to the salt mud tidal river and seashores, and all this evolution and transformation in one area, the Indo-Malayan one.

There is no sudden evolution of a flying organ or of adhesive apparatus; all is gradual—*Natura non facit saltum*. There is no stage in the evolution which is not an actual direct or immediate improvement in diffusion of species or genus. If we examine a number of fruits on a plant, we can see frequently that all are not exactly similar, and that they vary slightly in different directions; as environment alters, there is a selection made by Nature of those which are best adapted for the changed circumstances, and they fill the empty spaces. Seeds are constantly drifted by wind, water, or other ways, into vacant places, from open country to forest, and from forest to desert. Those that can

establish themselves are those that are more or less adapted for the altered conditions, and may, by the natural selection of improved forms, develop into a permanent and successful element of the local flora. Should the environment not alter, and the plant's method of dissemination be adequate, there is no further evolution necessary, and the fruit or seed does not evolve further; but if there is any considerable alteration of the environment, the dissemination methods must alter, or species will disappear. I do not mean that, in such case, dissemination is the only factor that must be modified—frequently all the organs and their physiology must be adapted to the changed circumstances—but I am only dealing with the question of dispersal.

The modifications by which the whole of the life-history of a species may be altered are often apparently very minute and trivial, though, in fact, they may have very far-reaching effects. The presence of a minute space between the cotyledons of a bean, for instance, makes the whole difference in the area of distribution of the species. Guppy has shown in some cases how some seeds of the same kind of plant possess this little air-space, and thereby are widely disseminated all over the tropics, from one coast to another and from one island to another, while in other seeds of the same plant the cotyledons are appressed together, and the seeds do not float, and have no such facility for migration. The firmer texture of the funicle in some seeds (e.g., *Laburnum*) causes them to remain attached to the valve till that is blown away by the winter winds, so that the seed is borne further on a wing formed by the valve. The position of the point of detachment of the ripe fruit, whether above or below the bracts (*Enkleia*, *Linnaea*), may make the whole difference to the distribution of the species. The period at which dehiscence of a leguminous pod takes place may affect the spread of the tree, and there are many more cases already detailed showing how very small adaptations have resulted in the abundance and the extensive migrations of plants.

I have given a general account of the methods of dispersal of plants, with numerous instances and observations to illustrate this, but a good deal more of field research is required to elucidate the complete history of dissemination of all the plants of the world. Of very many plants we know neither the habits nor habitats, nor their relations to their environment. Evolutionary modifications, however, are still continuing, and local floras are altering in many parts of the world, as ever they did. Records of these changes are still to be made by field naturalists, especially in the more distant and less known parts of the world.

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